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# Von Bertalanffy Growth Parameters of Non-Fish Marine Organisms

Fisheries Centre, University of British Columbia, Canada

# VON BERTALANFFY GROWTH PARAMETERS OF NON-FISH MARINE ORGANISMS

Edited by
Maria Lourdes D. Palomares and Daniel Pauly

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*A Research Report from the Fisheries Centre at UBC*

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# DIRECTOR'S FOREWORD

The report presented here is 'only' a compilation of growth and related parameters for marine, non-fish vertebrates and invertebrates, with only brief analyses, mainly to compare, and thus partly validate, the datasets. One could ask, what is the point? Why such compilation?

In the late 1970s, I undertook a similar compilation of growth parameters in fish [Pauly, D. 1978. A preliminary compilation of fish length growth parameters. *Berichte des Institut für Meereskunde an der Universität Kiel*, No. 55, 200 p.], one of the first of its kind. Its purpose, among other things, was to provide colleagues with a baseline against which to compare progress in the estimation of new growth parameters, whose absence was then perceived as a major impediment to the management of tropical fisheries. Within ten years, this compilation had morphed into the beginnings of FishBase. FishBase at first existed on various diskettes and CD-ROMs, then became an online database of fish - the only such database which not only presents the names and pretty picture of the species it covers, but also important features of their biology, such as, for example, their growth parameters (see www.fishbase.org).

The 7 papers of this report, which present growth parameters for marine mammals, seabirds, marine reptiles and many of the invertebrate tribes, however, will not lead to the creation of another database. This is so because a database and website have recently been created for non-fish marine metazoans. It is SeaLifeBase (www.sealifebase.org), which is patterned after FishBase, and which can therefore accommodate, in addition to the names of marine animals, any amount of biological information, notably growth and related parameters (length-weight relationships, size at first maturity, longevity, etc.).

Hence this report, in addition to its direct utility to readers, will serve as documentation for a large set of the growth parameters incorporated into SeaLifeBase. These parameters will be of interest to theoreticians, i.e., biologists who want to compare life history strategies in a wide range of taxa, and especially to ecosystem modelers, who need to populate their models with growth parameters and/or parameters derived from these, such as production/biomass ratios, an indication of productivity.

This report, therefore, endeavors to cover as wide a range of morphologies and ecological niches as possible. This was particularly successful for the non-fish vertebrates, of which all major groups are represented. For example, in the case of the reptilians, all marine families are represented, and most of the species, except for the very speciose sea snakes (Family Hydrophidae), for which, however, a very good sample of representative species is available.

The invertebrates, obviously, are the group for which we have the smallest sample relative to the number of extant species. The compilation that we have here, covering mainly commercial species from the Mediterranean is a good start, however, as are the two papers from the Western Central Pacific, with growth parameters for lobsters and oysters, respectively. Jointly with the growth parameters that were already included in SeaLifeBase, this should provide a starting point for most analyses.

# GROWTH OF MARINE MAMMALS[1]

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## ABSTRACT

Growth and length-weight data were obtained from the literature for 187 populations of 61 species of marine mammals ranging from sea otters to pygmy blue whales. Length-weight parameter estimates yielded a mean *b* value of 2.86. Estimates of the von Bertalanffy growth function indicate that smaller marine mammals, i.e., seals, sea lions, walruses and dolphins, tend to have growth performance indices between 3.5 to 4.5 and that larger marine mammals, i.e., male fur and elephant seals and whales, tend to have indices higher than 4.5. However, the auximetric plot of log K *vs* log $W_\infty$ shows a decreasing trend in growth performance, similar to that shown for fishes, seabirds and aquatic reptiles.

## INTRODUCTION

Interest in marine mammals, primarily harvesting and use of products derived from them (e.g., fur/hide, oil and meat), can be traced back to ancient times (Cotté & Guinet, 2007; Allen & Keay, 2006; Christensen, 2006; Tillman & Donovan, 1983). This interest evolved through time, graduating from the need to know of their seasonal whereabouts for obvious reasons connected to the hunt (Christensen, 2006), to a need to know how much fish they consume, i.e., the extent of their competition with fisheries (Kaschner & Pauly, 2005; Kastelein & Vaughan, 1989; Goode, 1884). For some rare species, interest is also growing as to the effect of climate change on their populations (see, e.g., Laidre *et al.*, 2006; Cotté & Guinet, 2007; Newsome *et al.*, 2007).

Studying animals living in aquatic environments has always been a challenge because of their inaccessibility to us, their observers. This inconvenience is compounded when the subject are marine mammals, many of which are highly migratory, or which can, on rare occasions, pose a threat to their human observers, as is the case with polar bears. Studying marine mammals is more difficult now that many have become in danger of extinction and, in most parts of the world, are protected species. Traditional life-history studies involve field sampling, and usually sacrificing a subset of the population being studied (see, e.g., True, 1885), or laboratory experiments following the life stages and growth of individual specimens. Nowadays, field sampling of marine mammal populations is done in the context of

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'scientific whaling' (see, e.g., Tamura & Konishi, 2006; Amano & Miyazaki, 2004; Bryden & Harrison, 1986) or when they are caught as by-catch (see, e.g., Miller *et al.*, 1998; Yoshida *et al.*, 1994; Bryden & Harrison, 1986), or stranded.

Marine mammal field studies, some dating back to the early 1970s (see, e.g., Stirling, 2002; Burns & Harbo, 1972), employed expensive field observation methods, e.g., helicopter observations or tagging and recapture methods, and were aimed primarily at collecting biogeographical data. There was no known method of determining ages of cetaceans and pinnipeds until the 1950s, and thus, the data required for growth analyses could not be obtained (Gaskin & Blair, 1977). This has changed, however, and length-at-age data are available and may be obtained from studies of: bones; GLG's (growth layer groups) of dentine, e.g., in odontocete cetaceans (Scheffer & Myrick, 1980); weight of eye lenses (Gaskin & Blair, 1977); track width measurements, e.g., in harbor seals (Reijnders 1976); amino acid racemisation (Bada *et al.*, 1980); counts of ovarian *corpora albicantia* (Kleinenberg & Klevezal, 1962); counts of periosteal bones (van Bree *et al.*, 1986; Brodie, 1969; Kleinenberg & Klevezal, 1962; Laws, 1960); and skeletal and external morphology (Stuart & Morejohn, 1980), e.g., in sea otters (Schneider, 1973). Such data were used to describe the growth of marine mammals using the Gompertz equation (Laird, 1969), logistic equations and, occasionally, the von Bertalanffy growth function (VBGF).

This paper assembles growth parameters for marine mammals, estimated using a variety of methods, and standardizes them using the VBGF, along with length-weight relationships. These life-history parameters are available through SeaLifeBase (www.sealifeabase.org), an information system on non-fish marine organisms patterned after the successful model for fish, FishBase (www.fishbase.org). Thus, a preliminary comparison of the growth performance of marine mammal can be presented.

## MATERIALS AND METHODS

### *Growth parameter estimation*

Growth parameters of marine mammal populations were obtained from published literature, and cover the following: (i) the parameters of growth equations other than the VBGF, notably the logistic and Gompertz curves; (ii) age-at-length or growth increment data; and (iii) time series of size frequency distributions. The parameters of the VBGF were recalculated from age-at-length data generated from (i), and all age-at-length and growth increment data were fitted to the VBGF (see von Bertalanffy, 1957) of the form:

$$L_t = L_\infty \left(1 - e^{-K\cdot(t-t_0)}\right) \qquad \ldots (1)$$

where $L_t$ is the length at age $t$, $L_\infty$ is the asymptotic length, i.e., the mean length the animal would reach if it could grow forever, $K$ is a coefficient of dimension $t^{-1}$, and $t_o$ is a parameter setting the origin of the curve on the age-axis.

Size frequency distributions were fitted to the Powell-Wetherall Plot (PW-Plot; see Pauly, 1998; Wetherall, 1986; Powell, 1979) to estimate $L_\infty$, based on the assumption that the resulting distribution is representative of the population. Plotting of successive mean lengths ($L_{mean}$), computed from successive cut-off lengths ($L_{i+1}$), minus the $L_i$ (i.e., $L_{mean}$- $L_i$) against $L_i$. The downward trend of the points were then fitted with a linear regression of the form $Y = a + bX$, with $L_\infty = a/-b$) and $Z/K = (1+b)/(-b)$, where $Z$ is the instantaneous rate of total mortality (Pauly, 1998). This method allows the estimation of $L_\infty$ and $Z/K$, i.e., exploited populations, where $Z$ is the instantaneous rate of total mortality. $Z/K$ is equivalent to $M/K$ in unexploited populations.

In cases where only $L_\infty$ estimates are available, e.g., results of the PW-Plot, values of $K$ were obtained using the growth performance index ($\Phi'$) defined by Pauly & Munro (1984) as $\Phi' = log_{10} K + 2\cdot log_{10}L_\infty$, and mean values of $\Phi'$, available from $L_\infty$ and $K$ pairs for: (a) the same species in different localities; (b) other species in the same genus; (c) other species in the same family. Growth parameters obtained through this method are marked as such in SeaLifeBase.

### *Asymptotic weight estimation*

Asymptotic weight, $W_\infty$, was estimated using the length-weight relationship of the form

$$W = a \cdot L^b \qquad \ldots (2)$$

where $a$ is a multiplicative term equivalent to the y-intercept of the log-log transformed linear regression, $L$ the length, and $b$ the exponent, equivalent to the slope of the regression. In many cases, sufficient length-weight data pairs were not available for linear regression analyses. Thus, condition factors (*c.f.*) using individual length-weight pairs were estimated with $c.f. = W \cdot 100/L^3$, where $W$ is the weight in grams, and $L$ the length in centimeters (Pauly, 1984). The value of the length-weight parameter $a$ was then obtained as $a = c.f./100$, assuming that $b$=3.

**Table 1.** Summary of marine mammal species and populations for which data on growth, length-weight relationships (L/W) and condition factors (*c.f.*) were obtained from the literature.

| Order | Family | Species | L/W | *c.f.* | VBGF |
|---|---|---|---|---|---|
| Carnivora | Mustelidae | 1 | - | 2 | 12 |
| | Odobenidae | 1 | - | 2 | 11 |
| | Otariidae | 10 | 8 | 17 | 24 |
| | Phocidae | 16 | 7 | 28 | 88 |
| | Ursidae | 1 | - | 2 | 2 |
| Cetacea | Balaenidae | 1 | - | 2 | 1 |
| | Balaenopteridae | 8 | 13 | 32 | 9 |
| | Delphinidae | 14 | 14 | 12 | 19 |
| | Eschrichtiidae | 1 | 1 | 4 | 1 |
| | Iniidae | 1 | - | 2 | 4 |
| | Monodontidae | 2 | 3 | 2 | 2 |
| | Phocoenidae | 3 | 3 | 4 | 11 |
| | Physeteridae | 1 | 3 | 11 | 3 |
| | Ziphiidae | 1 | 1 | - | - |

## RESULTS AND DISCUSSION

Our literature search, which relied heavily on Internet sources and electronic or 'soft' reprints, resulted in 173 length-weight relationships covering 61 species (Table A1), 187 asymptotic size estimates for 47 species and 179 $L_\infty$ and $K$ pairs for 46 species (Table A2). Table 1 summarizes the results obtained from this exercise. Note that only two estimates of Z/K were obtained (see Table A2 for values of Z/K calculated through the Powell-Wetherall Plot for the killer whale, *Orcinus orca* (Linnaeus, 1758)). The over-representation of phocids and otariids may be due to the fact that their populations remain on- or near-shore and are thus accessible for research. Among cetacean families, delphinids and balaenopterids are best represented. This may be a product of improved ageing techniques, but may also be a by product of whaling and fisheries by-catch. Few data are available for the oceanic Ziphiidae (Baird's beaked whale).

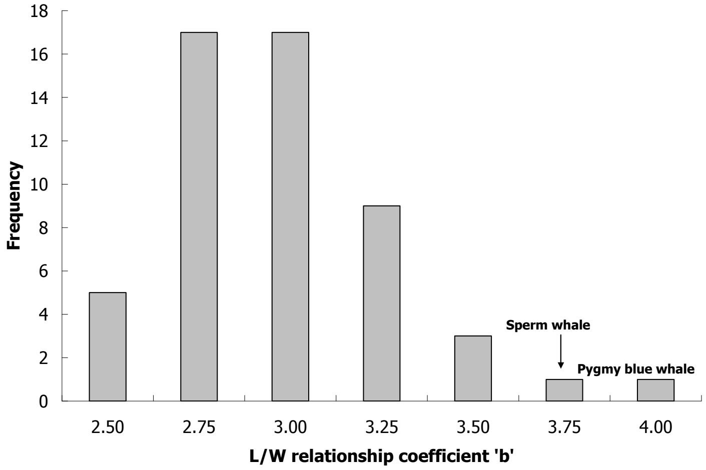

**Figure 1.** Frequency distribution of the length-weight relationship coefficient $b$ for 53 populations of marine mammals with length-weight data pairs (see Table A1 for details). Note that the outliers (pygmy blue and sperm whales) were obtained from Lockyer (1976; see Table A2 and text for discussion).

Asymptotic weights using equation (2) were obtained, based on the following criteria: i) species of the same sex, with length-weight and VBGF parameters from the same locality; ii) species from the same body of water; and iii) species with different sex/locality. Details of the methods used in solving for asymptotic weights are indicated in Table A2.

Values of the parameter $b$ of the length-weight relationship ranged from 2.31 to 3.97, with 120 estimates computed through condition factors (and the assumption of allometric growth; thus $b$=3), while 53 were obtained from regression analyses of several length-weight data pairs. Figure 1 shows the distribution of $b$

values for these 53 populations (mode at 2.74 and median at 2.86). The outliers at *b*=3.75 and 4.00 were obtained from Lockyer (1976, Table 1), which were based on weight of parts and not on whole individuals. Lockyer (1976) notes that fluid losses may account for the high *b* values and weights calculated from these L/W relationships. Discounting these outliers, we get a spread of *b* values between 2.50 and 3.50 with a mean at 2.86. This appears to justify our use of *b*=3 values to estimate the coefficient *a* from condition factors for other species for which several L/W data pairs are not available. Thus, we were able to obtain asymptotic weight values for all of the populations for which asymptotic length values were available (see Table A2).

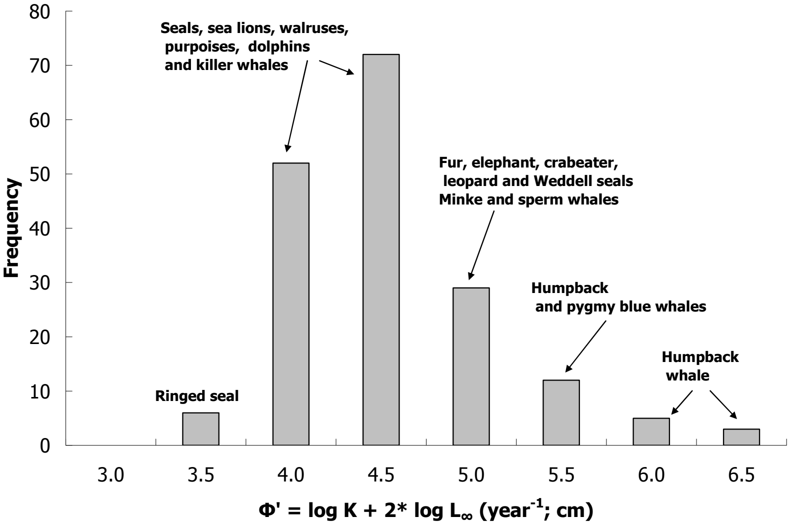

**Figure 2**. Frequency distribution of the growth performance index Φ' for 179 populations of marine mammals.

Asymptotic lengths ranged from 110 cm for a female *Enhydra lutris* (Linnaeus, 1758) (sea otter) from the Aleutian Islands (Alaska) to 2,190 cm for a female *Balaenoptera musculus brevicauda* (pygmy blue whale) from an unspecified location. The distribution of growth performance indices calculated for these 179 populations (Figure 2) indicated that, in general, seals, sea lions, walruses and dolphins (i.e., smaller

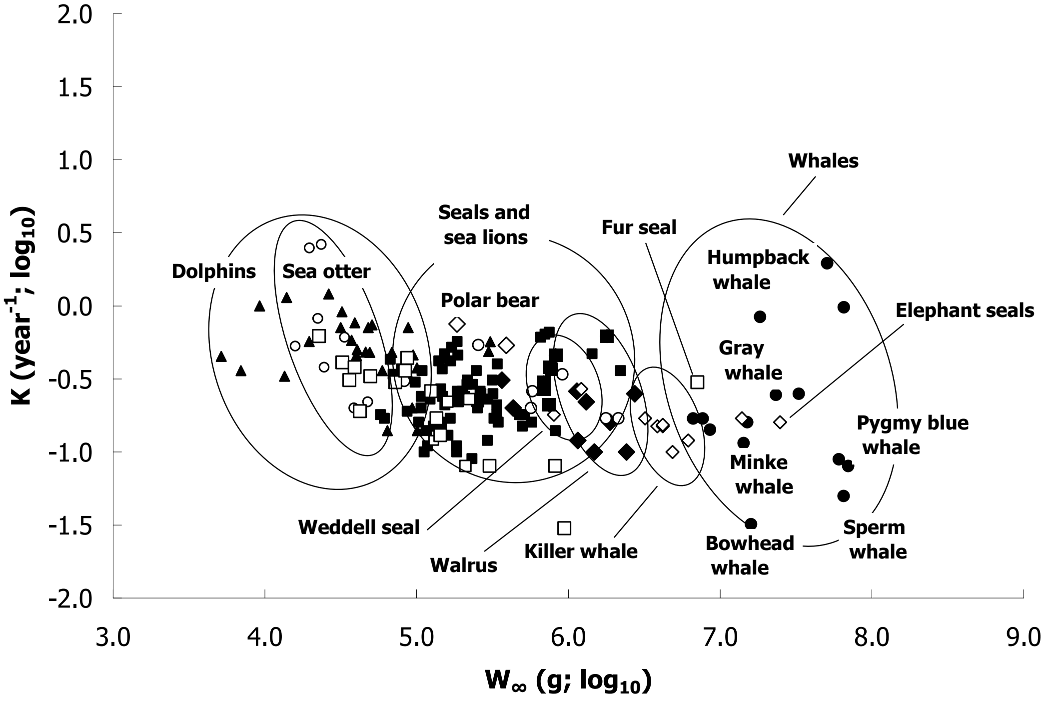

**Figure 3**. Auximetric plot of 179 populations of marine mammals (see Table A2 for details). Note that, in this plot, the growth of killer whales (which are basically large dolphins), and that of fur and elephant seals are similar to that of minke whales. Also note that the growth of polar bears is similar to that of seals and sea lions.

marine mammals), have indices between 3.5 and 4.5, while larger marine mammals tend to have indices higher than 4.5. These indices might be useful as a quick and easy test for the reliability of growth parameter estimates, notably in cases where the age-at-length or frequency distribution data might be biased or based on a small number of samples, not representing the population. Similarly, the auximetric plot of $W_\infty$ ($\log_{10}$; g) and $K$ ($\log_{10}$; year$^{-1}$;) in Figure 3, indicates that: a) sea otters, small species of dolphins, seals, sea lions and polar bears have similar growth patterns, typical of small marine mammals with $W_\infty$ ranging from $10^4$ to $10^5$ g; b) there is a medium sized group, i.e., walruses, Weddell seals, fur and elephant seals and killer whales, with $W_\infty$ ranging from $10^5$ to $10^7$ g; and c) the group of marine mammals, with $W_\infty$ ranging from $10^7$ to $10^8$ g, which include male fur and elephant seals and the great whales. Note that female fur and elephant seals grow in a fashion similar to sea otters, seals and sea lions. Figure 3 also indicates a downward trend in the growth performance of marine mammals, from smaller marine mammals with fast metabolic rates ($K$ values around 3.2 year$^{-1}$).

Overall, we find, as we did previously for fishes (Pauly *et al.*, 2000; Pauly, 1979), and, as we document in this report, for seabirds (Karpouzi & Pauly, 2008) and aquatic reptiles (Dar *et al.*, 2008), that auximetric plots (i.e., plots of $\log K$ *vs* $\log W_\infty$) can be used to show and interpret patterns in the growth of marine mammals.

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## Appendix

**Table A1.** Summary of 173 populations of 61 species of marine mammals for which length-weight relationships were found (t=tonnes; kg=kilograms; m=meters).

| Spec. No. | Species | Stock | Locality | Method | Sex | *b* | *a* | Source |
|---|---|---|---|---|---|---|---|---|
| 1 | *Arctocephalus australis*<br>(South American fur seal) | a | Rio Grande, Brazil | a from cf | F | 3.00 | 0.0488 | Fossi *et al*. (1997; Tab. 1) |
| | | b | Rio Grande, Brazil | a from mean cf | M | 3.00 | 0.0544 | idem |
| | | c | San Clemente, Argentina | a from cf | F | 3.00 | 0.0385 | idem |
| 2 | *Arctocephalus gazelle*<br>(Antarctic fur seal) | a | Not specified | a from cf | F | 3.00 | 0.0081 | Trites & Pauly (1998; Tab. 2) |
| | | b | Not specified | a from cf | M | 3.00 | 0.00396 | Idem |
| 3 | *Arctocephalus forsteri*<br>(New Zealand fur seal) | a | New Zealand | a from cf | F | 3.00 | 0.0191 | Dickie & Dawson (2003; p. 177) |
| | | b | New Zealand | a from cf | M | 3.00 | 0.0216 | idem |
| 4 | *Arctocephalus pusillus doriferus*<br>(Australian fur seal) | a | Seal Rocks, Bass Strait, Australia | Recomputed kg | F | 3.13 | 0.00993 | Arnould & Warneke (2002; p. 56) |
| | | b | Seal Rocks, Bass Strait, Australia | Recomputed from juv./adults, kg | M | 3.30 | 0.004726 | idem |
| 5 | *Arctocephalus tropicalis*<br>(Subantarctic fur seal) | a | Not specified | a from cf | F | 3.00 | 0.00841 | Trites & Pauly (1998; Tab. 2) |
| | | b | Not specified | a from cf | M | 3.00 | 0.00508 | idem |
| 6 | *Balaena mysticetus*<br>(bowhead whale) | a | Not specified | a from cf | F | 3.00 | 0.00384 | Trites & Pauly (1998; Tab 4) |
| | | b | Not specified | a from cf | male | 3.00 | 0.00393 | idem |
| 7 | *Balaenoptera acutorostrata*<br>(minke whale) | a | Washington | a from cf | F | 3.00 | 0.00927 | Lockyer (1976; p. 272) |
| | | b | Unspecified, Antarctic | a from mean cf | F | 3.00 | 0.0112 | idem |
| | | c | Unspecified, Antarctic | a from mean cf | M | 3.00 | 0.0133 | idem |
| | | d | Not specified | Recomputed from t and m | mixed | 2.31 | 1.189 | Lockyer (1976; Tab. 1) |
| | | e | Unspecified, Antarctic | a from mean cf | unsexed | 3.00 | 0.00687 | Lockyer (1976; p. 272) |
| | | f | Unspecified, Antarctic | Recomputed from t and m | unsexed | 3.23 | 0.00264 | Lockyer (1976; Tab. 2) |
| 8 | *Balaenoptera bonaerensis*<br>(Antarctic minke whale) | a | Southern Ocean | a from cf (pregnant) | F | 3.00 | 0.0115 | Tamura & Konishi (2006; Tab. 5) |
| | | b | Southern Ocean | a from cf | M | 3.00 | 0.0115 | idem |
| 9 | *Balaenoptera musculus brevicauda*<br>(pygmy blue whale) | a | Unspecified, Antarctic | a from cf | F | 3.00 | 0.00666 | Lockyer (1976; p. 269) |
| | | b | Unspecified, Antarctic | a from mean cf | M | 3.00 | 0.00644 | idem |
| | | c | Unspecified, Antarctic | Recomputed from t and m | mixed | 3.97 | 0.0000046 | Lockyer (1976; Tab. 2) |

**Table A1.** Continued.

| Spec. No. | Species | Stock | Locality | Method | Sex | *b* | *a* | Source |
|---|---|---|---|---|---|---|---|---|
| 10 | *Callorhinus ursinus* (northern fur seal) | a | Sanriku, Japan | a from mean cf | F | 3.00 | 0.019 | Ikemoto *et al*. (2004; Tab. 1) |
| | | b | Sanriku, Japan | a from mean cf | M | 3.00 | 0.0194 | Idem |
| | | c | Sanriku, Japan | a from mean cf | mixed | 3.00 | 0.019 | Idem |
| | | d | Not specified | | F | 2.74 | 0.0608 | Hunter (2005; Tab. A.8) |
| | | e | Not specified (pregnant) | | F | 2.67 | 0.0979 | idem |
| | | f | Not specified | | M | 2.83 | 0.0432 | idem |
| 11 | *Cystophora cristata* (hooded seal) | a | Not specified | a from cf | F | 3.00 | 0.0115 | Trites & Pauly (1998; Tab. 4) |
| | | b | Not specified | a from cf | M | 3.00 | 0.00471 | idem |
| 12 | *Delphinus delphis* (common dolphin) | a | Hawke Bay, North Island, New Zealand | a from mean cf | F | 3.00 | 0.0124 | Kastelein *et al*. (2000; Tab. 1) |
| | | b | Northeast, USA | a from mean cf | unsexed | 3.00 | 0.0119 | Kastelein *et al*. (2000; Tab. 3) |
| 13 | *Enhydra lutris* (sea otter) | a | western Alaska | a from cf | F | 3.00 | 0.0119 | Estes (1980, p. 2) |
| | | b | western Alaska | a from cf | M | 3.00 | 0.0147 | Idem |
| 14 | *Erignathus barbatus* (bearded seal) | a | Not specified | a from cf | F | 3.00 | 0.0107 | Trites & Pauly (1998; Tab. 2) |
| | | b | Not specified | a from cf | M | 3.00 | 0.0128 | Idem |
| 15 | *Eschrichtius robustus* (gray whale) | a | California, USA | a from mean cf | F | 3.00 | 0.0107 | Lockyer (1976; p. 268) |
| | | b | California, USA | a from mean cf | M | 3.00 | 0.00933 | Idem |
| | | c | California, USA | a from cf | unsexed | 3.00 | 0.0108 | Idem |
| | | d | Bering Sea | a from cf | F | 3.00 | 0.0131 | Idem |
| | | e | Northern Pacific | Recomputed from t and m | mixed | 3.28 | 0.0014 | Lockyer (1976; Tab. 2) |
| 16 | *Eumetopias jubatus* (steller sea lion) | a | Not specified | | F | 2.92 | 0.0332 | Hunter (2005; Tab. A.8) |
| | | b | Alaska | Recomputed from kg and m | F | 2.89 | 0.0363 | Idem |
| | | c | Alaska (pregnant) | Recomputed from kg and m | F | 2.79 | 0.0692 | Idem |
| 17 | *Grampus griseus* (Risso's dolphin) | a | Mediterranean Sea, Italy | Recomputed from kilograms | F | 3.00 | 0.0153 | Storelli & Marcotrigiano (2000; Tab. 1) |
| | | b | Mediterranean Sea, Italy | Recomputed from kilograms | F | 3.00 | 0.0152 | Idem |
| | | c | Mediterranean Sea, Italy | Recomputed from kilograms | F | 3.00 | 0.0146 | Idem |
| 18 | *Halichoerus grypus* (grey seal) | a | Not specified | | mixed | 2.86 | 0.0522 | Hunter (2005; Tab. A.8) |

**Table A1.** Continued.

| Spec. No. | Species | Stock | Locality | Method | Sex | *b* | *a* | Source |
|---|---|---|---|---|---|---|---|---|
| 19 | *Histriophoca fasciata* (ribbon seal) | a | Not specified | a from cf | F | 3.00 | 0.0104 | Trites & Pauly (1998; Tab. 4) |
| | | b | Not specified | a from cf | M | 3.00 | 0.0104 | Idem |
| 20 | *Hydrurga leptonyx* (leopard seal) | a | Not specified | a from cf | F | 3.00 | 0.0141 | Idem |
| | | b | Not specified | a from cf | M | 3.00 | 0.0117 | Idem |
| 21 | *Lagenodelphis hosei* (Fraser's dolphin) | a | Not specified | a from cf | mixed | 3.00 | 0.00519 | Idem |
| 22 | *Lagenorhynchus obliquidens* (Pacific white-sided dolphin) | a | Not specified | | mixed | 2.82 | 0.035 | Hunter (2005; Tab. A.8) |
| 23 | *Leptonychotes weddellii* (Weddell seal) | a | Unspecified, Antarctic | | mixed | 2.53 | 0.202 | Hunter (2005; Tab. A.8) |
| 24 | *Lobodon carcinophaga* (crabeater seal) | a | Not specified | a from cf | F | 3.00 | 0.0123 | Trites & Pauly (1998; Tab. 4) |
| | | b | Not specified | a from cf | M | 3 | 0.0112 | Idem |
| 25 | *Megaptera noveangliae* (humpback whale) | a | California, USA | a from mean cf | F | 3 | 0.0171 | Lockyer (1976; p. 272) |
| | | b | Unspecified, Antarctic | a from cf | F | 3 | 0.0103 | Idem |
| | | c | Unspecified, Antarctic | Recomputed from t and m | F | 2.95 | 0.0158 | Lockyer (1976; Tab. 2) |
| | | d | Puget Sound, Washington, USA | a from cf | F | 3 | 0.0104 | Lockyer (1976; p. 272) |
| | | e | Bering Sea | a from cf | F | 3 | 0.0121 | Idem |
| | | f | Bering Sea | a from cf | M | 3 | 0.0129 | Lockyer (1976; p. 272) |
| | | g | Not specified | Recomputed from t and m | mixed | 2.95 | 0.062 | Lockyer (1976; Tab. 1) |
| 26 | *Mirounga angustirostris* (northern elephant seal) | a | Año Nuevo State Reserve, California, USA | Recomputed from kg and m | M | 3.02 | 0.0281 | Haley *et al.* (1991; Tab. 1) |
| 27 | *Mirounga leonine* (southern elephant seal) | a | Not specified | a from cf | F | 3 | 0.0116 | Trites & Pauly (1998; Tab. 2) |
| | | b | Not specified | a from cf | M | 3 | 0.00462 | Idem |
| 28 | *Monachus schauinslandi* (Hawaiian monk seal) | a | Not specified | a from cf | F | 3 | 0.0118 | Trites & Pauly (1998; Tab. 4) |
| | | b | Not specified | a from cf | M | 3 | 0.0106 | Idem |
| 29 | *Monodon monoceros* (narwhal) | a | Western Greenland | a from mean cf | F | 3 | 0.0161 | Garde *et al.* (2007, p. 57-58) |
| | | b | Western Greenland | a from mean cf | M | 3 | 0.0168 | Idem |
| 30 | *Neophocaena phocaenoides* (finless porpoise) | a | Kyushu around Nagasaki and Kanmon Pass, Japan | a from mean cf | F | 3 | 0.0157 | Shirakihara *et al.* (1993; Tab. 2) |
| | | b | Kyushu around Nagasaki and Kanmon Pass, Japan | a from mean cf | M | 3 | 0.0144 | Shirakihara *et al.* (1993; Tab. 3) |
| | | c | Not specified | a from cf | mixed | 3 | 0.00576 | Trites & Pauly (1998; Tab. 4) |

**Table A1.** Continued.

| Spec. No. | Species | Stock | Locality | Method | Sex | *b* | *a* | Source |
|---|---|---|---|---|---|---|---|---|
| 31 | *Odobenus rosmarus* (walrus) | a | Not specified | a from cf | F | 3 | 0.0175 | Trites & Pauly (1998; Tab. 2) |
| | | b | Not specified | a from cf | M | 3 | 0.0143 | Idem |
| 32 | *Orcinus orca* (killer whale) | a | Not specified | | mixed | 3.2 | 0.006 | Hunter (2005; Tab. A.8) |
| | | b | Not specified | | mixed | 2.58 | 0.208 | Idem |
| 33 | *Otaria flavescens* (South American sea lion) | a | Not specified | a from cf | F | 3 | 0.0113 | Trites & Pauly (1998; Tab. 4) |
| | | b | Not specified | a from cf | M | 3 | 0.00469 | Idem |
| 34 | *Pagophilus groenlandicus* (harp seal) | a | Not specified | | mixed | 2.81 | 0.0645 | Hunter (2005; Tab. A.8) |
| 35 | *Phoca largha* (larga seal) | a | Not specified | a from cf | F | 3 | 0.0095 | Trites & Pauly (1998; Tab. 4) |
| | | b | Not specified | a from cf | M | 3 | 0.0102 | Idem |
| 36 | *Phoca vitulina* (Harbour seal) | a | Not specified | | mixed | 2.89 | 0.0404 | Hunter (2005; Tab. A.8) |
| 37 | *Phocoena phocoena* (harbour porpoise) | a | Not specified | | F | 2.43 | 0.216 | Idem |
| | | b | Not specified | | M | 2.74 | 0.051 | Idem |
| | | c | Not specified | | mixed | 2.63 | 0.083 | Hunter (2005; Tab. A.8) |
| 38 | *Phocoenoides dalli* (Dall's porpoise) | a | Not specified | a from cf | mixed | 3 | 0.00576 | Trites & Pauly (1998; Tab. 4) |
| 39 | *Physeter macrocephalus* (sperm whale) | a | Japan | a from mean cf | F | 3 | 0.00893 | Lockyer (1976; p. 273) |
| | | b | Japan | a from mean cf | M | 3 | 0.00964 | Lockyer (1976; p. 272-273) |
| | | c | Japan | Recomputed from t and m | mixed | 3.18 | 0.0029 | Lockyer (1976; Tab. 1) |
| | | d | Natal, South Africa | a from mean cf | F | 3 | 0.0131 | Lockyer (1976; p. 273) |
| | | e | Natal, South Africa | Recomputed from t and m | F | 3.55 | 0.00023 | Lockyer (1976; Tab. 2) |
| | | f | Natal, South Africa | a from cf | M | 3 | 0.0131 | Lockyer (1976; p. 273) |
| | | g | Bering Sea | a from mean cf | M | 3 | 0.00918 | Idem |
| | | h | Bering Sea | a from mean cf | unsexed | 3 | 0.00797 | Idem |
| | | i | Iceland | a from cf | M | 3 | 0.00997 | Idem |
| | | j | Canada | a from cf | M | 3 | 0.0139 | Idem |
| | | k | Antarctic and Pacific | Recomputed from t and m | mixed | 2.74 | 0.0649 | Lockyer (1976; Tab. 2) |
| | | l | Unspecified, Antarctic | a from mean cf | unsexed | 3 | 0.0109 | Lockyer (1976; p. 273) |
| | | m | Not specified | a from cf | F | 3 | 0.00584 | Trites & Pauly (1998; Tab. 2) |
| | | n | Not specified | a from cf | M | 3 | 0.00462 | Idem |
| 40 | *Pontoporia blainvillei* (franciscana dolphin) | a | Not specified | a from cf | F | 3 | 0.00626 | Idem |
| | | b | Not specified | a from cf | M | 3 | 0.00635 | Idem |

**Table A1.** Continued.

| Spec. No. | Species | Stock | Locality | Method | Sex | *b* | *a* | Source |
|---|---|---|---|---|---|---|---|---|
| 41 | *Pusa caspica* (Caspian seal) | a | Caspian Sea | a from cf | F | 3 | 0.0341 | Ikemoto *et al.* (2004; Tab. 1) |
| | | b | Caspian Sea | a from cf | M | 3 | 0.0285 | Idem |
| | | c | Caspian Sea | a from cf | mixed | 3 | 0.033 | Idem |
| | | d | northern Caspian Sea | a from mean cf | F | 3 | 0.031 | Watanabe *et al.* (2002;Tab. 1) |
| | | e | northern Caspian Sea | a from mean cf (pregnant) | F | 3 | 0.0362 | Idem |
| | | f | northern Caspian Sea | a from mean cf (non-pregnant) | F | 3 | 0.027 | Idem |
| | | g | northern Caspian Sea | a from mean cf | M | 3 | 0.0327 | Idem |
| 42 | *Pusa hispida* (ringed seal) | a | Svalbard | Recomputed from kg and m | F | 3.15 | 0.0145 | Hunter (2005; Tab. A.8) |
| | | b | Svalbard | Recomputed from kg and m | M | 3.26 | 0.00832 | Idem |
| | | c | Kongsfjorden, Svalbard | Recomputed from kilograms | F | 3 | 0.0257 | Krafft *et al.* (2007; Tab. 2) |
| | | d | Kongsfjorden, Svalbard | Recomputed from kilograms | male | 3 | 0.0350 | Idem |
| 43 | *Pusa sibirica* (Baikal seal) | a | Lake Baikal | a from mean cf | F | 3 | 0.0248 | Ikemoto *et al.* (2004; Tab. 1) |
| | | b | Lake Baikal | a from mean cf | M | 3 | 0.021 | Idem |
| | | c | Lake Baikal | a from mean cf | mixed | 3 | 0.023 | Idem |
| 44 | *Stenella frontalis* (Atlantic spotted dolphin) | a | Not specified | a from cf | F | 3 | 0.00562 | Trites & Pauly (1998; Tab. 4) |
| | | b | Not specified | a from cf | M | 3 | 0.00567 | Idem |
| 45 | *Steno bredanensis* (rough-toothed dolphin) | a | Not specified | a from cf | F | 3 | 0.00529 | Idem |
| | | b | Not specified | a from cf | M | 3 | 0.00518 | Idem |
| 46 | *Tursiops truncates* (bottlenose dolphin) | a | Not specified | a from cf | F | 3 | 0.00348 | Trites & Pauly (1998; Tab. 2) |
| | | b | Not specified | a from cf | M | 3 | 0.00367 | Idem |
| 47 | *Ursus maritimus* (polar bear) | a | Svalbard | a from cf | F | 3 | 0.0253 | Derocher & Wiig (2002; Tab. 1) |
| | | b | Svalbard | a from cf | M | 3 | 0.0342 | Idem |
| 48 | *Arctocephalus pusillus* (South African fur seal) | a | Not specified | a from cf | F | 3 | 0.0101 | Trites & Pauly (1998; Tab. 4) |
| | | b | Not specified | a from cf | M | 3 | 0.00444 | Idem |
| 49 | *Arctocephalus townsendi* (Guadalupe fur seal) | a | Guadalupe, Mexico | a from mean cf | F | 3 | 0.0151 | Gallo-Reynoso *et al.* (1996; Table 1) |

**Table A1.** Continued.

| Spec. No. | Species | Stock | Locality | Method | Sex | *b* | *a* | Source |
|---|---|---|---|---|---|---|---|---|
| 50 | *Balaenoptera borealis* (sei whale) | a | Japan | a from mean cf | F | 3 | 0.00559 | Lockyer (1976; p. 271) |
| | | b | Japan | a from mean cf | M | 3 | 0.00617 | Lockyer (1976; p. 270) |
| | | c | Japan | Recomputed from t and m | mixed | 2.43 | 0.356 | Lockyer (1976; Tab. 1) |
| | | d | Japan | Recomputed from t and m | unsexed | 2.43 | 0.334 | Lockyer (1976; Tab. 2) |
| | | e | Natal, South Africa | a from cf | F | 3 | 0.00856 | Lockyer (1976; p. 271) |
| | | f | Unspecified, Antarctic | a from cf | M | 3 | 0.00639 | Idem |
| 51 | *Balaenoptera brydei* (Bryde's whale) | a | Japan | a from mean cf | F | 3 | 0.00622 | Idem |
| | | b | Japan | a from mean cf | M | 3 | 0.00623 | Idem |
| | | c | Japan | Recomputed from t and m | mixed | 2.74 | 0.0429 | Lockyer (1976; Tab. 1) |
| | | d | Japan | Recomputed from t and m | unsexed | 2.74 | 0.0404 | Lockyer (1976; Tab. 2) |
| 52 | *Balaenoptera musculus* (blue whale) | a | Unspecified, Antarctic | a from mean cf | F | 3 | 0.00612 | Lockyer (1976; p. 269) |
| | | b | Unspecified, Antarctic | a from mean cf | M | 3 | 0.00636 | Lockyer (1976; p. 268-269) |
| | | c | Unspecified, Antarctic | Recomputed from t and m | mixed | 3.09 | 0.00304 | Lockyer (1976; Tab. 2) |
| | | d | Unspecified, Antarctic | a from mean cf | unsexed | 3 | 0.00593 | Lockyer (1976; p. 269) |
| | | e | Not specified | Recomputed from t and m | mixed | 3.25 | 0.000917 | Lockyer (1976; Tab. 1) |
| | | f | Newfoundland, Canada | a from cf | unsexed | 3 | 0.00473 | Lockyer (1976; p. 269) |
| 53 | *Balaenoptera physalus* (fin whale) | a | Unspecified, Antarctic | a from mean cf | F | 3 | 0.00554 | Lockyer (1976; p. 270) |
| | | b | Unspecified, Antarctic | a from mean cf | M | 3 | 0.0056 | Lockyer (1976; p. 270) |
| | | c | Unspecified, Antarctic | Recomputed from t and m | unsexed | 2.53 | 0.207 | Lockyer (1976; Tab. 2) |
| | | d | California, USA | a from cf | F | 3 | 0.00581 | Lockyer (1976; p. 270) |
| | | e | Korf Bay, Kamchatka, Russia | a from cf | F | 3 | 0.00598 | Idem |
| | | f | Natal'ya Bay, Russia | a from cf | F | 3 | 0.00617 | Idem |
| | | g | Far East | a from cf | F | 3 | 0.00619 | Idem |
| | | h | Far East | a from cf | M | 3 | 0.00583 | Lockyer (1976; p. 269) |
| | | i | Iceland | a from mean cf | M | 3 | 0.00573 | Idem |
| | | j | Commander Island, Russia | a from cf | M | 3 | 0.00504 | Idem |
| | | k | Not specified | Recomputed from t and m | mixed | 2.9 | 0.0127 | Lockyer (1976; Tab. 1) |
| 54 | *Berardius bairdii* (Baird's beaked whale) | a | Japan | | mixed | 3.08 | 0.00634 | Hunter (2005; Tab. A.8) |

**Table A1.** Continued.

| Spec. No. | Species | Stock | Locality | Method | Sex | *b* | *a* | Source |
|---|---|---|---|---|---|---|---|---|
| 55 | *Cephalorhynchus hectori* (Hector's dolphin) | a | Not specified | | mixed | 2.53 | 0.1689 | Idem |
| 56 | *Delphinapterus leucas* (white whale) | a | St. Lawrence, Canada | | mixed | 2.61 | 0.156 | Idem |
| | | b | Hudson Bay, Canada | | mixed | 2.56 | 0.182 | Idem |
| | | c | Hudson Bay, Canada | | mixed | 2.54 | 0.452 | Idem |
| 57 | *Globicephala melas* (long-finned pilot whale) | a | Faeroe Island (postnatal) | | mixed | 2.5 | 0.23 | Idem |
| 58 | *Pseudorca crassidens* (false killer whale) | a | Not specified | | mixed | 2.44 | 0.216 | Idem |
| 59 | *Stenella attenuate* (Pantropical spotted dolphin) | a | Not specified | | F | 2.61 | 0.0696 | Idem |
| | | b | Not specified | | M | 2.87 | 0.0193 | Idem |
| | | c | Not specified | | mixed | 2.93 | 0.0126 | Idem |
| 60 | *Stenella coeruleoalba* (striped dolphin) | a | Not specified (postnatal) | | F | 2.91 | 0.0183 | Idem |
| | | b | Not specified (postnatal) | | M | 2.98 | 0.0139 | Idem |
| | | c | Not specified | | mixed | 2.93 | 0.0171 | Idem |
| 61 | *Stenella longirostris* (long-snouted spinner dolphin) | a | Not specified | | F | 2.61 | 0.0696 | Idem |
| | | b | Not specified | | M | 2.87 | 0.0193 | Idem |

**Table A2**. Summary of 179 populations of 47 marine mammal species for which von Bertalanffy growth parameters were found.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | K (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | *Arctocephalus australis* (South American fur seal) | a | Isla de Lobos, Uruguay | 253 | F | 118 | 72 | 0.30 | -0.67 | Length-at-age; 0-28.5 years. Average $W_\infty$ from Tab. 1 (1a, 1c). Lima & Paez (1995; Fig. 1). |
| 2 | *Arctocephalus gazelle* (Antarctic fur seal) | a | Not specified | - | F | 220 | 87 | 0.44 | -0.68 | From generalized VBGF. $W_\infty$ from Tab. 1(2b). McLaren (1993; Tab. 1). |
| | | b | Idem | - | M | 331 | 143 | 0.13 | -0.66 | Idem |
| 3 | *Arctocephalus forsteri* (New Zealand fur seal) | a | New Zealand | 57 | F | 119 | 32 | 0.41 | - | $W_\infty$ from Tab. 1 (3a). Dickie & Dawson (2003; Tab. 1). |
| | | b | Kangaroo Island, South Australia | - | F | 137 | 50 | 0.33 | -1.55 | $W_\infty$ from Tab. 1(3a). McKenzie *et al.* (2007; Tab. 2). |
| | | c | Idem | - | M | 184 | 135 | 0.17 | -8.18 | $W_\infty$ from Tab. 1 (3b). McKenzie *et al.* (2007; Tab. 2). |
| 4 | *Arctocephalus pusillus doriferus* (Australian fur seal) | a | Seal Rocks, Bass Strait, Australia | 163 | F | 163 | 84 | 0.36 | -1.91 | $W_\infty$ from Tab. 1 (4a). Arnould & Warneke (2002; Tab. 1) |
| | | b | Idem | 69 | M | 600 | 7072 | 0.30 | -0.88 | From logistic curve. $W_\infty$ from Tab. 1(4b). Arnould & Warneke (2002, Abstract); Hunter (2005; Tab. A.8). |
| 5 | *Arctocephalus tropicalis (Subantarctic fur seal)* | a | Amsterdam Island, southern Indian Ocean | 108 | F | 139 | 23 | 0.62 | - | From Gompertz equation. $W_\infty$ from Tab. 1 (5a). Dabin *et al.* (2004; p. 1045). |
| 6 | *Balaena mysticetus* (bowhead whale) | a | Alaska | - | unsexed | 1602 | 16000 | 0.032 | -22.2 | Average $W_\infty$ from Tab. 1 (6a, 6b). George *et al.* (1999; p. 575) |
| 7 | *Balaenoptera acutorostrata* (minke whale) | a | Not specified | - | M | 833 | 7688 | 0.17 | -4.30 | $W_\infty$ from Tab. 1 (7c). Hunter (2005, Tab. A.8). |
| 8 | *Balaenoptera bonaerensis* (Antarctic minke whale) | a | Idem | - | F | 907 | 8581 | 0.14 | -4.30 | $W_\infty$ from Tab. 1 (8a). Hunter (2005, Tab. A.8). |
| | | b | Idem | - | ♂ | 833 | 6647 | 0.17 | -4.30 | $W_\infty$ from Tab. 1(8b). Hunter (2005, Tab. A.8). |
| 9 | *Balaenoptera musculus brevicauda* (pygmy blue whale) | a | Idem | 170 | F | 2190 | 70000 | 0.08 | -16.2 | From m to cm. $W_\infty$ from Tab. 1 (9a). Branch (2008, Tab. 3). |
| | | b | Idem | 218 | M | 2110 | 60500 | 0.09 | -15.5 | From m to cm. $W_\infty$ from Tab. 1 (9b). Branch (2008, Tab. 3). |
| 10 | *Callorhinus ursinus (northern fur seal)* | a | Eastern Bering Sea, California | 6493 | F | 128 | 36 | 0.31 | -2.06 | Length at age; non-pregnant females; 0-15 years.Average $W_\infty$ from Tab. 1 (10a, 10d-e). Trites & Bigg (1996; Tab. 1). |
| | | b | Idem | 9630 | F | 130 | 42 | 0.19 | -7.32 | Length at age; pregnant females; 4-23 years. Average $W_\infty$ from Tab. 1 (10a, 10d-e). Trites & Bigg (1996; Tab. 1). |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | K (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 10 | *Callorhinus ursinus* (northern fur seal) | c | Idem | 2008 | M | 266 | 303 | 0.08 | -3.69 | Length at age; 0-16 years. W∞ from Tab. (10b, 10f). Trites & Bigg (1996; Tab. 1). |
| | | d | Pribilof Island, Alaska | 137 | F | 127 | 39 | 0.38 | -1.83 | Length at age; 0-10 years. Average W∞ from Tab. 1 (10a, 10d-e). Scheffer & Wilke (1953; Tabs. 1-2). |
| | | e | Idem | 306 | M | 308 | 818 | 0.08 | -3.13 | Length at age; 0-10 years. Average W∞ from Tab. 1 (10b, 10f). Scheffer & Wilke (1953; Tabs. 1-2). |
| | | f | Not specified | - | F | 198 | 124 | 0.26 | -0.67 | From generalized VBGF. Average W∞ from Tab. 1 (10d-e). McLaren (1993; Tab. 1). |
| | | g | Idem | - | M | 396 | 942 | 0.03 | -0.42 | From generalized VBGF. W∞ from Tab. 1 (10f). McLaren (1993; Tab. 1) |
| 11 | *Cystophora cristata* (hooded seal) | a | Idem | - | F | 280 | 252 | 0.20 | -0.62 | From generalized VBGF. W∞ from Tab. 1 (11a). McLaren (1993; Tab. 1). |
| | | b | Idem | - | M | 311 | 141 | 0.16 | -0.61 | From generalized VBGF. W∞ from Tab. 1 (11b). McLaren (1993; Tab. 1). |
| 12 | *Delphinus delphis* (common dolphin) | a | Hawke Bay, North Island, New Zealand | 4 | F | 196 | 93 | 0.20 | -6.99 | Length at age; 2-27 years. W∞ from Tab. 1 (12a). Kastelein *et al.* (2000; Fig. 3). |
| 13 | *Enhydra lutris* (sea otter) | a | Not specified | - | F | 148 | 39 | 0.20 | - | L∞ from $L_{max}$; K from theta of female pups (13c). W∞ from Tab. 1 (13a). Jefferson *et al.* (1993). |
| | | b | Idem | - | M | 148 | 48 | 0.22 | - | L∞ from maximum length; K from theta of female pups (13c). W∞ from Tab. 1 (13b). Jefferson *et al.* (1993). |
| | | c | Western Aleutian Islands, Alaska | 102 | F | 118 | 20 | 2.49 | -0.22 | Length at age; female pups; 0-3 years. W∞ from Tab. 1 (13a). Schneider (1973; Tab. 3). |
| | | d | Idem | 90 | M | 117 | 24 | 2.63 | -0.21 | Length at age; male pups; 0-3 years. W∞ from Tab. 1 (13b). Schneider (1973; Tab. 3). |
| | | e | Aleutian Islands, Alaska | - | F | 110 | 16 | 0.53 | -2.35 | W∞ from Tab. 1 (13a). Laidre *et al.* (2006; Tab. 2). |
| | | f | Idem | - | F | 123 | 22 | 0.82 | -1.55 | Idem |
| | | g | Idem | - | M | 119 | 25 | 0.38 | -2.51 | W∞ from Tab. 1 (13b). Laidre *et al.* (2006; Tab. 2). |
| | | h | Idem | - | M | 132 | 33 | 0.61 | -2.05 | Idem |
| | | i | California, USA | - | F | 128 | 25 | - | - | W∞ from Tab. 1 (13a). Laidre *et al.* (2006; p. 985). |
| | | j | Idem | - | F | 127 | 24 | - | - | Idem |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | $K$ (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 13 | *Enhydra lutris* (sea otter) | k | Idem | - | M | 119 | 25 | - | - | $W_\infty$ from Tab. 1 (13b). Laidre *et al.* (2006; p. 985). |
| | | l | Idem | - | M | 118 | 24 | - | - | Idem |
| 14 | *Erignathus barbatus* (bearded seal) | a | Barents Sea | - | mixed | 306 | 338 | 0.21 | -0.70 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (14a-b). McLaren (1993; Tab. 1). |
| | | b | Sea of Okhotsk | - | mixed | 271 | 233 | 0.29 | -0.74 | Idem |
| | | c | Bering-Chukchi Sea | - | mixed | 300 | 319 | 0.25 | -0.71 | Idem |
| | | d | Eastern Canada | - | mixed | 326 | 516 | 0.18 | -0.73 | Idem |
| 15 | *Eschrichtius robustus* (gray whale) | a | California and Washington, USA | - | F | 1297 | 23346 | 0.25 | -2.84 | $W_\infty$ from Tab. 1 (15a). Kastelle *et al.* (2003; p. 26). |
| 16 | *Eumetopias jubatus* (steller sea lion) | a | Gulf of Alaska | - | F | 360 | 913 | 0.34 | -0.65 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (16b-c). McLaren (1993; Tab. 1). |
| | | b | Idem | - | M | 486 | 2137 | 0.17 | -0.65 | Idem |
| | | c | Shelikof Alaska | - | F | 304 | 567 | 0.20 | -0.66 | Idem |
| | | d | Idem | - | M | 454 | 1766 | 0.17 | -0.64 | Idem |
| | | e | Alaska | 201 | F | 230 | 255 | 0.54 | -1.05 | Length at age; 0-24 years. Average $W_\infty$ from Tab. 1 (16b-c). Winship *et al.* (2001; Tab. 3). |
| | | f | Idem | 235 | M | 307 | 579 | 0.26 | -1.50 | Length at age; 0-18 years. Average $W_\infty$ from Tab. 1 (16b-c). Winship *et al.* (2001; Tab. 3). |
| 17 | *Grampus griseus* (Risso's dolphin) | a | Taiji, Japan | - | F | 271 | 298 | 0.49 | -2.09 | Average $W_\infty$ from Tab. 1 (17a-c). Amano & Miyazaki (2004; Fig. 2). |
| | | b | Idem | - | M | 273 | 305 | 0.57 | -1.62 | Idem |
| 18 | *Halichoerus grypus* (grey seal) | a | Eastern Canada | - | F | 271 | 475 | 0.18 | -0.60 | From generalized VBGF. $W_\infty$ from Tab. 1 (18a). McLaren (1993; Tab. 1). |
| | | b | Idem | - | M | 328 | 821 | 0.14 | -0.58 | Idem |
| | | c | Farne Islands, England | - | F | 241 | 338 | 0.18 | -0.53 | Idem |
| | | d | Idem | - | M | 290 | 573 | 0.16 | -0.54 | Idem |
| 19 | *Histriophoca fasciata* (ribbon seal) | a | Sea of Okhotsk | - | F | 245 | 153 | 0.47 | -0.62 | From generalized VBGF. $W_\infty$ from Tab. 1 (19a). McLaren (1993; Tab. 1). |
| | | b | Idem | - | M | 261 | 185 | 0.57 | -0.62 | Idem |
| | | c | Idem | - | mixed | 254 | 17 | 0.52 | -0.64 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (19a-b). McLaren (1993; Tab. 1). |
| | | d | Bering Sea | - | F | 242 | 148 | 0.37 | -0.63 | From generalized VBGF. $W_\infty$ from Tab. 1 (19a). McLaren (1993; Tab. 1). |
| | | e | Idem | - | M | 262 | 187 | 0.46 | -0.64 | From generalized VBGF. $W_\infty$ from Tab. 1 (19b). McLaren (1993; Tab. 1). |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | $K$ (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 19 | *Histriophoca fasciata* (ribbon seal) | f | Idem | - | mixed | 253 | 168 | 0.42 | -0.63 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (19a-b). McLaren (1993; Tab. 1). |
| 20 | *Hydrurga leptonyx* (leopard seal) | a | Antarctic | - | F | 539 | 221 | 0.36 | -0.69 | From generalized VBGF. $W_\infty$ from Tab. 1 (20a). McLaren (1993; Tab. 1). |
| | | b | Idem | - | M | 497 | 1434 | 0.47 | -0.69 | From generalized VBGF. $W_\infty$ from Tab. 1 (20b). McLaren (1993; Tab. 1). |
| 21 | *Lagenodelphis hosei* (Fraser's dolphin) | a | Southeast Brazil | 11 | mixed | 236 | 69 | 0.48 | -1.05 | Length at age; 0-19 years. $W_\infty$ from Tab. 1 (21a). Siciliano *et al.* (2007; Tab. 6). |
| 22 | *Lagenorhynchus obliquidens* (Pacific white-sided dolphin) | a | North Pacific | - | F | 186 | 88 | 0.71 | -1.29 | $W_\infty$ from Tab. 1 (22a). Heise (1997; Tab. 2). |
| | | b | Idem | - | M | 195 | 100 | 0.38 | -2.06 | Idem |
| | | c | Idem | - | mixed | 191 | 95 | 0.46 | -1.75 | $W_\infty$ from Tab. 1 (22a). Hunter (2005; Tab. A8). |
| 23 | *Leptonychotes weddellii* (Weddell seal) | a | South Orkney Island | - | F | 558 | 1795 | 0.62 | -0.73 | From generalized VBGF. $W_\infty$ from Tab. 1 (23a). McLaren (1993; Tab. 1). |
| | | b | McMurdo Sound, Antarctica | - | F | 399 | 770 | 0.37 | -0.73 | Idem |
| | | c | Idem | - | F | 394 | 743 | 0.21 | -0.74 | Idem |
| | | d | Idem | - | M | 410 | 824 | 0.46 | -0.73 | Idem |
| | | e | Idem | - | M | 382 | 687 | 0.30 | -0.73 | Idem |
| | | f | Idem | - | mixed | 396 | 756 | 0.38 | -0.72 | Idem |
| | | g | Idem | - | mixed | 383 | 692 | 0.27 | -0.74 | Idem |
| 24 | *Lobodon carcinophaga* (crabeater seal) | a | Not specified | - | F | 393 | 747 | 0.66 | -0.73 | From generalized VBGF. $W_\infty$ from Tab. 1 (24a). McLaren (1993; Tab. 1). |
| | | b | Idem | - | M | 389 | 659 | 0.61 | -0.74 | From generalized VBGF. $W_\infty$ from Tab. 1 (24b). McLaren (1993; Tab. 1). |
| | | c | Idem | - | mixed | 391 | 702 | 0.64 | -0.72 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (24a-b). McLaren (1993; Tab. 1). |
| 25 | *Megaptera novaeangliae* (humpback whale) | a | Northwest Atlantic | - | mixed | 1050 | 51000 | 1.96 | -0.26 | From generalized VBGF. $W_\infty$ from Tab. 1 (25g). Stevick (1999; Fig. 4). |
| | | b | Idem | - | mixed | 1145 | 65410 | 0.98 | -0.46 | Idem |
| | | c | Northern Atlantic | 11 | F | 1394 | 33000 | 0.25 | -3.18 | Length at age; not a good fit. Average $W_\infty$ from Tab. 1 (25a, 25f). Stevick (1999; Tab. 1). |
| | | d | Idem | 12 | M | 1124 | 18327 | 0.84 | -1.00 | Length at age; not a good fit. $W_\infty$ from Tab. 1 (25f). Stevick (1999; Tab. 1). |
| 26 | *Mirounga angustirostris* (northern elephant seal) | a | Not specified | - | F | 492 | 3851 | 0.15 | -0.67 | From generalized VBGF. $W_\infty$ from Tab. 1 (26a). McLaren (1993; Tab. 1). |
| | | b | Idem | - | M | 911 | 250000 | 0.16 | -0.68 | Idem |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | $K$ (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 27 | *Mirounga leonine* (southern elephant seal) | a | Macquarie Island | - | F | 410 | 802 | 0.18 | -0.68 | From generalized VBGF. $W_\infty$ from Tab. 1 (27a). McLaren (1993; Tab. 1). |
| | | b | South Georgia | - | F | 471 | 12147 | 0.27 | -0.67 | Idem |
| | | c | Idem | - | M | 1444 | 14000 | 0.17 | -0.68 | From generalized VBGF. $W_\infty$ from Tab. 1 (27b). McLaren (1993; Tab. 1). |
| 28 | *Monachus schauinslandi* (Hawaiian monk seal) | a | Not specified | - | mixed | 354 | 497 | 0.15 | -0.73 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (28a-b). McLaren (1993; Tab. 1). |
| 29 | *Monodon monoceros* (narwhal) | a | West Greenland | 24 | F | 396 | 1000 | - | - | $W_\infty$ from Tab. 1 (29a). Garde *et al.* (2007; p. 52). |
| | | b | Idem | 38 | M | 457 | 1603 | - | - | $W_\infty$ from Tab. 1 (29b). Garde *et al.* (2007; p. 52). |
| 30 | *Neophocaena phocaenoides* (finless porpoise) | a | Kyushu, Japan | 46 | F | 148 | 51 | 0.74 | -1.00 | Length at age. $W_\infty$ from Tab. 1 (30a). Shirakihara *et al.* (1993; Tab. 1). |
| | | b | Idem | 51 | M | 150 | 48 | 0.71 | -1.00 | Length at age. $W_\infty$ from Tab. 1 (30b). Shirakihara *et al.* (1993; Tab. 1). |
| 31 | *Odobenus rosmarus* (walrus) | a | Foxe Basin, Northwest Territories, Canada | 90 | F | 275 | 364 | 0.31 | -1.86 | $W_\infty$ from Tab. 1 (31a). Garlich-Miller & Stewart (1998; Tab. 1). |
| | | b | Idem | 103 | M | 312 | 433 | 0.20 | -2.71 | $W_\infty$ from Tab. 1 (31b). Garlich-Miller & Stewart (1998; Tab. 1). |
| | | c | Foxe Basin, Nunavut, Canada | - | M | 576 | 2735 | 0.25 | -0.86 | From generalized VBGF. $W_\infty$ from Tab. 1 (31b). McLaren (1993; Tab. 1). |
| | | d | Hudson Bay, Canada | - | F | 402 | 1137 | 0.26 | -0.87 | From generalized VBGF. $W_\infty$ from Tab. 1 (31a). McLaren (1993; Tab. 1). |
| | | e | Idem | - | M | 432 | 1153 | 0.12 | -0.87 | From generalized VBGF. $W_\infty$ from Tab. 1 (31b). McLaren (1993; Tab. 1). |
| | | f | Unspecified, Alaska | - | F | 422 | 1311 | 0.22 | -0.87 | From generalized VBGF. $W_\infty$ from Tab. 1 (31a). McLaren (1993; Tab. 1). |
| | | g | Idem | - | M | 470 | 1481 | 0.10 | -0.87 | From generalized VBGF. $W_\infty$ from Tab. 1 (31b). McLaren (1993; Tab. 1). |
| | | h | Unspecified, Russia | - | F | 475 | 1879 | 0.16 | -0.88 | From generalized VBGF. $W_\infty$ from Tab. 1 (31a). McLaren (1993; Tab. 1). |
| | | i | Idem | - | M | 552 | 2411 | 0.10 | -0.87 | From generalized VBGF. $W_\infty$ from Tab. 1 (31b). McLaren (1993; Tab. 1). |
| 31 | *Odobenus rosmarus* (walrus) | j | Northwest Greenland | 34 | F | 269 | 341 | - | - | $W_\infty$ from Tab. 1 (31a). Knutsen & Born (1994). |
| | | k | Idem | 54 | M | 314 | 443 | - | - | $W_\infty$ from Tab. 1 (31b). Knutsen & Born (1994). |
| 32 | *Orcinus orca* (killer whale) | a | Norway, coastal waters | 173 | F | 564 | 3196 | 0.17 | -4.17 | Length at age. Average $W_\infty$ from Tab. 1 (32a-b). Christensen (1984; Fig. 4). |
| | | b | Idem | 143 | M | 650 | 4854 | 0.10 | -5.81 | Idem |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | *K* (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 32 | *Orcinus orca* (killer whale) | c | British Columbia and Washington | 27 | F | 618 | 4180 | 0.15 | - | $L_\infty$ from Powell-Wetherall Plot; K from theta (32e). Z/K=0.628. Average $W_\infty$ from Tab. 1 (32a-b). Bigg & Wolman (1975). |
| | | d | Idem | 29 | M | 704 | 6151 | 0.12 | - | $L_\infty$ from Powell-Wetherall Plot; K from theta (32e). Z/K=1.05. Average $W_\infty$ from Tab. 1 (32a-b). Bigg & Wolman (1975). |
| | | e | Holland, Netherlands | 1 | F | 618 | 4180 | 0.15 | - | Growth increments; Gulland and Holt Plot; 1-12 years. Average $W_\infty$ from Tab. 1 (32a-b). Kastelein & Vaughan (1989; Tab. 1). |
| 33 | *Otaria flavescens* (South American sea lion) | a | Southern Brazil | 32 | F | 194 | 83 | 0.31 | -2.00 | $W_\infty$ from Tab. 1 (33a). Rosas *et al.* (1993; p. 141, 143). |
| | | b | Idem | 94 | M | 254 | 77 | 0.30 | -1.60 | $W_\infty$ from Tab. 1 (33b). Rosas *et al.* (1993; p. 141, 143). |
| 34 | *Pagophilus groenlandicus* (harp seal) | a | Not specified | - | mixed | 240 | 315 | 0.31 | -0.57 | From generalized VBGF. $W_\infty$ from Tab. 1 (34a). McLaren (1993; Tab. 1). |
| 35 | *Phoca largha* (larga seal) | a | Bering-Okhotsk Sea | - | F | 225 | 109 | 0.36 | -0.56 | From generalized VBGF. $W_\infty$ from Tab. 1 (35a). McLaren (1993; Tab. 1). |
| 35 | *Phoca largha* (larga seal) | b | Idem | - | M | 246 | 152 | 0.44 | -0.53 | From generalized VBGF. $W_\infty$ from Tab. 1 (35b). McLaren (1993; Tab. 1). |
| | | c | Hokkaido, Japan | - | F | 209 | 87 | 0.19 | -0.57 | From generalized VBGF. $W_\infty$ from Tab. 1 (35a). McLaren (1993; Tab. 1). |
| | | d | Idem | - | M | 216 | 103 | 0.16 | -0.55 | From generalized VBGF. $W_\infty$ from Tab. 1 (35b). McLaren (1993; Tab. 1). |
| 36 | *Phoca vitulina* (Harbour seal) | a | Commander, Aleutian and Pribilof Islands | - | F | 167 | 107 | 0.20 | -4.49 | From generalized VBGF. $W_\infty$ from Tab. 1 (36a). McLaren (1993; Fig. 40). |
| | | b | Idem | - | M | 175 | 123 | 0.23 | -3.80 | Idem |
| | | c | Norway | - | F | 210 | 207 | 0.24 | -0.63 | Idem |
| | | d | Idem | | M | 226 | 256 | 0.22 | -0.65 | Idem |
| | | e | Gulf of Alaska | - | F | 203 | 189 | 0.22 | -0.64 | From generalized VBGF. $W_\infty$ from Tab. 1 (36a). McLaren (1993; Fig. 39). |
| | | f | Idem | - | F | 150 | 78 | 0.31 | -3.03 | Idem |
| | | g | Idem | - | M | 162 | 98 | 0.30 | -2.76 | Idem |
| | | h | Idem | - | M | 226 | 257 | 0.22 | -0.62 | Idem |
| | | i | Aleutian, Alaska | - | F | 218 | 231 | 0.09 | -0.66 | Idem |
| | | j | Idem | - | M | 245 | 323 | 0.17 | -0.65 | Idem |
| | | k | Denmark/Sweden | - | F | 207 | 200 | 0.26 | -0.62 | Idem |
| | | l | Idem | - | M | 228 | 263 | 0.26 | -0.63 | Idem |
| | | m | Nova Scotia, Canada | - | F | 223 | 247 | 0.36 | -0.63 | Idem |
| | | n | Idem | - | M | 249 | 340 | 0.40 | -0.63 | Idem |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | $K$ (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 36 | *Phoca vitulina* (Harbour seal) | o | British Columbia | - | F | 217 | 227 | 0.23 | -0.64 | From generalized VBGF. $W_\infty$ from Tab. 1 (36a). McLaren (1993; Fig. 38). |
| | | p | Idem | - | F | 236 | 292 | 0.12 | -0.65 | Idem |
| | | q | Idem | - | F | 151 | 79 | 0.37 | -2.52 | Idem |
| | | r | Idem | - | M | 167 | 108 | 0.24 | -3.69 | Idem |
| | | s | Hokkaido, Japan | - | F | 224 | 249 | 0.22 | -0.62 | Idem |
| | | t | Idem | - | M | 250 | 345 | 0.16 | -0.64 | Idem |
| 37 | *Phocoena phocoena* (Harbour porpoise) | a | Sea of Azov | 45 | F | 145 | 39 | 0.76 | - | $W_\infty$ from Tab. 1(37a). Gol'din (2004; Tab. 1). |
| | | b | Idem | 53 | M | 132 | 32 | 0.91 | - | $W_\infty$ from Tab. 1(37b). Gol'din (2004; Tab. 1). |
| | | c | Black Sea | 41 | F | 132 | 32 | 0.71 | - | $W_\infty$ from Tab. 1(37a). Gol'din (2004; Tab. 1). |
| | | d | Idem | 48 | M | 123 | 26 | 1.21 | - | $W_\infty$ from Tab. 1(37b). Gol'din (2004; Tab. 1). |
| | | e | Western Greenland | - | F | 155 | 46 | 0.48 | - | $W_\infty$ from Tab. 1(37a). Lockyer *et al.* (2001; Tab. 3). |
| | | f | Idem | - | M | 143 | 40 | 0.46 | - | $W_\infty$ from Tab. 1(37b). Lockyer *et al.* (2001; Tab. 3). |
| 38 | *Phocoenoides dalli* (Dall's porpoise) | a | Western Aleutian Islands | - | F | 186 | 37 | 0.58 | -1.39 | Length-at-age. $W_\infty$ from Tab. 1 (38a). Ferrero & Walker (1999; Figs. 8-9). |
| | | b | Idem | - | F | 188 | 38 | 0.40 | -2.78 | Idem |
| | | c | Idem | - | M | 192 | 41 | 0.50 | -1.60 | Idem |
| 39 | *Physeter macrocephalus* (Sperm whale) | a | Tasmania, Australia | - | F | 1082 | 15100 | 0.16 | -2.58 | Average $W_\infty$ from Tab. 1 (39d-e). Evans *et al.* (2004; p. 248). |
| | | b | Western Australia | - | mixed | 1052 | 14300 | 0.12 | -4.12 | Average $W_\infty$ from Tab. 1 (39d-e). Bannister (1969). |
| | | c | Not specified | - | M | 1858 | 65100 | 0.05 | -5.37 | Length-at-age. Average $W_\infty$ from Tab. 1 (39a-n). Lockyer (1981; Abstract). |
| 40 | *Pontoporia blainvillei* (Franciscana dolphin) | a | Paraná and Sao Paulo (25°00' - 25°58'S), Brazil | 18 | F | 129 | 13 | 0.33 | -3.07 | $W_\infty$ from Tab. 1 (40a). Barreto & Rosas (2006; Tab. 3). |
| | | b | Idem | 23 | M | 113 | 9 | 1.00 | -0.90 | $W_\infty$ from Tab. 1 (40b). Barreto & Rosas (2006; Tab. 3). |
| | | c | Rio Grande do Sul (29°20' - 33°45'S), Brazil | 48 | F | 146 | 20 | 0.57 | -1.71 | $W_\infty$ from Tab. 1 (40a). Barreto & Rosas (2006; Tab. 3). |
| | | d | Idem | 59 | M | 130 | 14 | 1.14 | -0.71 | $W_\infty$ from Tab. 1 (40b). Barreto & Rosas (2006; Tab. 3). |
| 41 | *Pusa caspica (Caspian seal)* | a | Not specified | | F | 185 | 202 | 0.25 | -0.61 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (41a, 41d-f). McLaren (1993; Tab. 1). |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | $K$ (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 42 | *Pusa hispida (ringed seal)* | a | Sea of Okhotsk |  | F | 161 | 118 | 0.11 | -0.62 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a, 42c). McLaren (1993; Tab. 1). |
|  |  | aa | High Canada, Arctic |  | mixed | 181 | 184 | 0.1 | -0.61 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a-d). McLaren (1993; Tab. 1). |
|  |  | b | Sea of Okhotsk |  | M | 164 | 146 | 0.15 | -0.61 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42b, 42d). McLaren (1993; Tab. 1). |
|  |  | c | Idem |  | mixed | 162 | 130 | 0.12 | -0.63 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a-d). McLaren (1993; Tab. 1). |
|  |  | d | Chukchi Sea |  | F | 172 | 144 | 0.27 | -0.58 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a, 42c). McLaren (1993; Tab. 1) |
|  |  | e | Idem |  | M | 167 | 154 | 0.21 | -0.6 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42b, 42d). McLaren (1993; Tab. 1) |
|  |  | f | Idem |  | mixed | 169 | 149 | 0.24 | -0.61 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a-d). McLaren (1993; Tab. 1) |
|  |  | g | Baltic Sea |  | F | 198 | 222 | 0.23 | -0.63 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a, 42c). McLaren (1993; Tab. 1) |
|  |  | h | Baltic Sea |  | M | 205 | 294 | 0.23 | -0.62 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42b, 42d). McLaren (1993; Tab. 1). |
|  |  | i | Idem |  | mixed | 204 | 265 | 0.25 | -0.61 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a-d). McLaren (1993; Tab. 1). |
|  |  | j | Barents Sea |  | F | 178 | 160 | 0.22 | -0.62 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a, 42c). McLaren (1993; Tab. 1) |
|  |  | k | Idem |  | M | 186 | 215 | 0.29 | -0.61 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42b, 42d). McLaren (1993; Tab. 1). |
|  |  | l | Idem |  | mixed | 181 | 185 | 0.26 | -0.63 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a-d). McLaren (1993; Tab. 1). |
|  |  | m | Bering Sea |  | F | 180 | 167 | 0.17 | -0.6 | From generalized VBGF. Average $W_\infty$ from Tab. 1 (42a, 42c). McLaren (1993; Tab. 1) |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | $K$ (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 42 | *Pusa hispida (ringed seal)* | n | Idem | | M | 184 | 210 | 0.08 | -0.61 | From generalized VBGF. Average W∞ from Tab. 1 (42b, 42d). McLaren (1993; Tab. 1). |
| | | o | Idem | | mixed | 180 | 183 | 0.11 | -0.56 | From generalized VBGF. Average W∞ from Tab. 1 (42a-d). McLaren (1993; Tab. 1). |
| | | p | Svalbard | | F | 166 | 129 | 0.15 | -0.58 | From generalized VBGF. Average W∞ from Tab. 1 (42a, 42c). McLaren (1993; Tab. 1) |
| | | q | Idem | 144 | F | 130 | 61 | 0.17 | | Average W∞ from Tab. 1 (42a, 42c). Krafft *et al.* (2006; Tab 1). |
| | | r | Idem | 102 | F | 128 | 58 | 0.18 | | Idem |
| | | s | Idem | 131 | M | 130 | 70 | 0.34 | | Average W∞ from Tab. 1 (42b, 42d). Krafft *et al.* (2006; Tab 1). |
| | | t | Idem | 170 | M | 128 | 67 | 0.43 | | Idem |
| | | u | Idem | | M | 186 | 216 | 0.31 | -0.62 | From generalized VBGF. Average W∞ from Tab. 1 (42b, 42d). McLaren (1993; Tab. 1). |
| | | v | Idem | | mixed | 172 | 157 | 0.22 | -0.6 | From generalized VBGF. Average W∞ from Tab. 1 (42a-d). McLaren (1993; Tab. 1). |
| | | w | Western Canada, Arctic | | F | 160 | 116 | 0.14 | -0.65 | From generalized VBGF. Average W∞ from Tab. 1 (42a, 42c). McLaren (1993; Tab. 1) |
| | | x | Western Canada, Arctic | | M | 169 | 161 | 0.13 | -0.67 | From generalized VBGF. Average W∞ from Tab. 1 (42b, 42d). McLaren (1993; Tab. 1). |
| | | y | Idem | | mixed | 164 | 136 | 0.15 | -0.68 | From generalized VBGF. Average W∞ from Tab. 1 (42a-d). McLaren (1993; Tab. 1). |
| | | z | Southeast Canada, Arctic | | mixed | 154 | 112 | 0.1 | -0.59 | Idem |
| 43 | *Pusa sibirica* (Baikal seal) | a | Not specified | | F | 178 | 140 | 0.42 | -0.62 | From generalized VBGF. Average W∞ from Tab. 1 (43a). McLaren (1993; Tab. 1). |
| 44 | *Stenella frontalis* (Atlantic spotted dolphin) | a | Southeast Brazil | 27 | mixed | 225 | 64 | 0.14 | -5.56 | Length at age; 0-23 years. Average W∞ from Tab. 1 (44a-b). Siciliano *et al.* (2007; Tab. 1). |
| 45 | *Steno bredanensis* (rough-toothed dolphin) | a | Idem | 13 | mixed | 259 | 91 | 0.32 | -2.97 | Length at age; 0.5-24 years. Average W∞ from Tab. 1 (45a-b). Siciliano *et al.* (2007; Tab. 5). |

**Table A2**. Continued.

| Spec. No. | Species | Stock | Locality | N | Sex | $L_\infty$ (cm) | $W_\infty$ (kg) | $K$ (year$^{-1}$) | $t_o$ (year) | Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|
| 46 | *Tursiops truncates* (bottlenose dolphin) | a | Idem | 21 | mixed | 305 | 101 | 0.14 | -6.24 | Length at age; 0-26 years. Average W∞ from Tab. 1 (46a-b). Siciliano *et al.* (2007; Tab. 3). |
| | | b | North-Central Gulf of Mexico | | F | 242 | 49 | 0.48 | -1.19 | From Gompertz curve; <1-30 years. W∞ from Tab. 1 (46a). Mattson *et al.* (2006; Fig. 6). |
| | | c | Idem | | M | 253 | 59 | 0.36 | -1.77 | From Gompertz curve; <1-30 years. W∞ from Tab. 1 (46b). Mattson *et al.* (2006; Fig. 6). |
| | | d | Indian River Lagoon, Florida, USA | 72 | F | 114 | 5 | 0.45 | | From Gompertz equation. W∞ from Tab. 1 (46a). Stolen *et al.* (2002; Tab. 1). |
| | | e | Idem | 118 | M | 124 | 7 | 0.36 | -0.01 | From Gompertz equation. W∞ from Tab. 1 (46b). Stolen *et al.* (2002; Tab. 1). |
| 47 | *Ursus maritimus* (polar bear) | a | Svalbard | | F | 194 | 185 | 0.75 | -0.27 | W∞ from Tab. 1 (47a). Hunter (2005; Tab. A.8). |
| | | b | Idem | | M | 225 | 390 | 0.537 | -0.4 | W∞ from Tab. 1 (47b). Hunter (2005; Tab. A.8) |

# LIFE-HISTORY PATTERNS IN MARINE BIRDS[1]

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## ABSTRACT

The parameters of the von Bertalanffy growth equation for seabirds were estimated from previously published growth curves to allow within and between group comparisons of their life-history patterns. Overall, growth data were available for 447 seabird populations breeding around the globe, corresponding to 137 species, 13 families and four orders. A negative relationship between the logarithmic values of $W_\infty$ and K was identified for the orders of Charadriiformes, Pelecaniformes, Procellariiformes, and Sphenisciformes, as well as all seabird species combined. The values of the slope b ranged from -0.32 for the Sphenisciformes, to -0.12 for the Pelecaniformes, with a mean slope of -0.21, when all seabirds were considered.

## INTRODUCTION

Seabirds can be broadly characterized as long-lived species, with delayed sexual maturation and breeding, as well as low annual reproductive rates. Many species have a life span well over 30 years (e.g., most species of albatrosses; Schreiber & Burger, 2002). In addition, most species start breeding when they are three years or older (e.g., over ten years in some albatross species; Schreiber and Burger, 2002). Most species lay not more than three eggs, and in some instances chick rearing lasts for a long time (e.g., 380 days in the Wandering albatross; Schreiber & Burger, 2002).

These life-history characteristics have been shaped as an evolutionary response to conditions of living in the marine environment, i.e, reflecting the patchy and unpredictable distribution of marine resources (Ricklefs, 1990; Hamer *et al.*, 2002; Weimerskirch, 2002), which poses challenges to seabirds in finding food and provisioning chicks. Nonetheless, Weimerskirch (2007) has recently suggested that prey dispersal may not be as unpredictable as we once thought. As a result, specialization of seabirds for use of a particular marine habitat may be the driving force for the evolution of a particular life history strategy (Weimerskirch, 2007).

Life-history strategies have been studied for a number of marine organisms (fish: e.g., Adams, 1980; Froese & Pauly, 1998; Pauly, 1998; Stergiou, 2000; marine mammals: e.g., Herzing, 1997; Trites & Pauly, 1998; sea turtles: e.g., Fraser & Ehrhart, 1985; van Buskirk & Crowder, 1994; marine birds: e.g., Ricklefs, 1990; Visser, 2002; Weimerskirch, 2007). In addition, examining relationships between life history traits and developing empirical equations has been proven useful for comparisons among different taxonomic groups (e.g., Peters, 1983; Froese & Pauly, 1998; Visser, 2002). Growth, in particular, has been described in seabirds with the use of several mathematical equations. Three of the most popular ones are listed in Table 1 (see also Table 8.1 in Peters, 1983). For all three equations, parameters are estimated by fitting the selected model to size-at-age data for each individual or population under study. These equations allow

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the estimation of the key parameters of chick growth, such as the growth constant, $K$, and the asymptotic weight, $W_\infty$ and a measure of how rapidly this approached ($K_I$, $K_G$, $K$).

In the present study, we compiled information on growth parameters of seabird chicks, in an attempt to explore their life-history patterns. In addition, we established empirical relationships between life-history traits, in order to investigate potential differences in growth rates for a few seabird orders.

**Table 1:** Three equations most frequently used to describe chick growth in marine birds.

| Growth curve | Equation | Description |
|---|---|---|
| 1) Logistic | $W_t = W_\infty / (1 + e^{-K_L \cdot (t-t_L)})$ | $W_\infty$: asymptotic weight;<br>$K_L$: logistic growth rate constant;<br>$t_L$: the time of inflection point, which corresponds to the age of 50% of asymptotic weight of chicks. |
| 2) Gompertz | $W_t = W_\infty \cdot e^{-e^{-K_G \cdot (t-t_G)}}$ | $W_\infty$: asymptotic weight;<br>$K_G$: Gompertz growth rate constant;<br>$t_G$: the time of inflection point. |
| 3) Von Bertalanffy (VB) | $W_t = W_\infty \cdot (1 - e^{-K \cdot (t-t_0)})^b$ | $W_\infty$: asymptotic weight;<br>$K$: VB growth rate constant;<br>$t_o$: the theoretical 'age' the chick would have at weight zero;<br>$b$: exponent indicating isometric growth pattern, when its value is 3. |

## METHODOLOGY

In the present study, we gathered all available information pertinent to growth patterns in seabird chicks, from studies conducted since 1937. Overall, growth data were available for 447 seabird populations, corresponding to 137 species, 13 families and four orders (Tables 2 to 4). For the purpose of this paper, we defined as seabird population a number of seabirds belonging to the same species and breeding at a certain location at a certain year (Tables 2 to 4). We gathered information using the following databases: (a) Aquatic Sciences and Fisheries Abstracts; (b) Web of Science - Thomson Scientific; (c) BioSciences Information Service of Biological Abstracts; and (d) the Searchable Ornithological Research Archive, which cover peer-reviewed journals and other literature sources. We also used some unpublished theses and technical reports that were available to us, and extracted information from the online database of Birds of North America, Cornell University (http://bna.birds.cornell.edu/BNA/).

The form of the VBGF used here is:

$$W_t = W_\infty \cdot (1\text{-}e^{-K \cdot (t-t0)})^3 \qquad \ldots 1)$$

where $W_t$ is the weight at age $t$, $W_\infty$ the asymptotic size (here the size of a chick if it were to continue growing forever in the manner described by the equation), $K$ is a parameter of dimension time$^{-1}$ (here: year$^{-1}$), and $t_o$ adjusts the function such that $W_t$=0 at $t$=$t_o$.

In case where the original graph of chick body weight-at-age was not available, we obtained data for the following life-history parameters, to fit the VBGF: (a) the asymptotic weight, $W_\infty$ (g), the growth constant, $K_L$ (in days$^{-1}$), and the inflection point, $t_L$ (in days), of the logistic growth curve (Table 2); and (b) the asymptotic weight, $W_\infty$ (in g), the growth constant, $K_G$ (in days-1), and the inflection point, $t_G$ (in days), of the Gompertz growth curve (Table 3). When information on $K_L$ and $t_L$ was not available, we used the following equations respectively to estimate the missing values:

$$K_L = 0.962 \cdot W_\infty^{-0.31} \qquad \ldots 2$$

(Visser, 2002); and

$$t_L = \ln (W_\infty/W0 - 1) / K_L \qquad \ldots 3)$$

where $W_0$ is the initial weight of the chicks at hatching (Navarro and Bucher, 1990).

For each seabird population, we calculated seven data points of time when chick body weight is equal to 1%, 5%, 10%, 25%, 50%, 75%, 90%, 95%, and 99% of $W_\infty$, using the growth curve published by the corresponding study, and then used these data points to re-express growth parameters in terms of the VBGF (see Figure 1 for examples). As the VBGF and the other growth functions share one parameter ($W_\infty$), we kept this constant, and used the least square optimization technique to estimate the other VBGF parameters ($K$, $t_0$), given the data points. An example is given in Figure 1, for the growth of the Crested auklet (*Aethia cristatella*) chicks of the Okhotsk Sea (Figure 1a), and of the Least auklet (*Aethia pussila*) chicks of the Pribilof Islands, Alaska (Figure 1b).

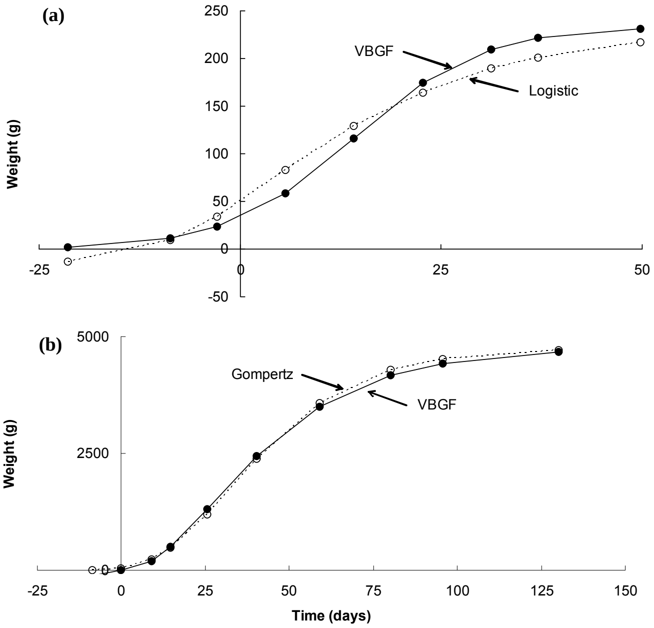

**Figure 1.** Comparison of the von Bertalanffy growth function (VBGF; black dot, solid line) with the growth curve originally used (open dot, dotted line) to describe weight-at-age data (not shown). (a) Crested auklet (*Aethia cristatella*) from the Okhotsk Sea, described with the logistic growth function (Kitaysky, 1999). (b) Light-mantled albatross (*Phoebetria palpebrata*) from Macquarie Island, Southern Ocean, described with the Gompertz growth function (Terauds and Gales, 2006).

When the chick body weight-at-age graph was provided in the original studies, data was traced and re-analyzed using the least square optimization technique to get growth parameter estimates in terms of the VBGF. An example is given in Figure 2, for the growth of Little shearwater (*Puffinus assimilis*) chicks of New Zealand.

The standard deviation (*SD*) was also estimated as a measure of effectiveness of the least-squares optimization. For all seabird populations, *SD* was then re-expressed as a % deviation (%D), i.e., relative to $W_t$=0.5* $W_\infty$.

Pauly *et al.* (1996) proposed the auximetric plot as another tool for the comparison of within- and between- species growth patterns. The auximetric plot is a double logarithmic plot of the parameters K and the asymptotic size ($W_\infty$ or $L_\infty$) (Pauly *et al.*, 1996; Froese and Pauly, 2000). In such a plot, each set of growth parameters represents a point, with the different points for a species or higher taxon forming an ellipsoid cluster of points, whose surface area is related to the 'growth space' occupied by a given species or higher taxon (Pauly *et al.*, 1996; Froese and Pauly, 2000).

**Table 2.** Growth parameters of seabird chicks from the logistic growth curve (in normal font), and also estimated for this paper (in bold), using the von Bertalanffy (VB) growth model. $W_\infty$ (in g): asymptotic weight of chicks for both the logistic and VB growth models; $t_l$ (in days): inflection point of logistic curve; $t_o$ (in years): hypothetical 'age' chicks would have had at zero weight; $K_l$ (in days$^{-1}$) and $K$ (in years$^{-1}$): growth coefficients for the logistic and VB models respectively. AK: Alaska; CA: California; WA: Washington State; and NY: New York State.

| **Species** | **Area (Year)** | $t_l$ | $K_l$ | $W_\infty$ | $K$ | $t_o$ | **Source** |
|---|---|---|---|---|---|---|---|
| **Alcidae** | | | | | | | |
| *Aethia cristatella* | Okhotsk Sea (1994) | 14.17 | 0.129 | 233 | **20.96** | **-0.043** | Kitaysky (1999) |
| *Cepphus columba* | Farallon Is, AK (1989) | *14.01 | ¤0.150 | 401 | **24.37** | **-0.032** | Shultz and Sydeman (1997) |
| *Cepphus columba* | Farallon Is, AK (1990) | *12.75 | ¤0.155 | 359 | **25.19** | **-0.033** | Shultz and Sydeman (1997) |
| *Cepphus columba* | Farallon Is, AK (1991) | *15.86 | ¤0.143 | 466 | **23.24** | **-0.031** | Shultz and Sydeman (1997) |
| *Cepphus columba* | Farallon Is, AK (1992) | *15.90 | ¤0.143 | 468 | **23.24** | **-0.031** | Shultz and Sydeman (1997) |
| *Cepphus columba* | Farallon Is, AK (1993) | *15.91 | ¤0.143 | 469 | **23.24** | **-0.031** | Shultz and Sydeman (1997) |
| *Cepphus columba* | Farallon Is, AK (1994) | *13.95 | ¤0.150 | 398 | **24.37** | **-0.032** | Shultz and Sydeman (1997) |
| *Cepphus columba* | Farallon Is, AK (1995) | *15.26 | ¤0.145 | 443 | **23.56** | **-0.031** | Shultz and Sydeman (1997) |
| *Cerorhinca monocerata* | Destruction Is, WA (1974) | *23.20 | 0.074 | 335 | **12.02** | **-0.080** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Destruction Is, WA (1975) | *27.74 | 0.068 | 395 | **11.05** | **-0.080** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Destruction Is, WA (1979) | *32.78 | 0.058 | 400 | **9.43** | **-0.093** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Destruction Is, WA (1980) | *38.44 | 0.049 | 394 | **7.96** | **-0.111** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Destruction Is, WA (1981) | *39.49 | 0.049 | 412 | **7.96** | **-0.108** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Protection Is, WA (1975) | *24.61 | 0.076 | 412 | **12.35** | **-0.072** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Protection Is, WA (1976) | *27.71 | 0.071 | 432 | **11.54** | **-0.073** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Protection Is, WA (1979) | *25.88 | 0.076 | 432 | **12.35** | **-0.069** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Protection Is, WA (1980) | *25.15 | 0.078 | 430 | **12.67** | **-0.067** | Wilson and Manuwal (1986) |
| *Cerorhinca monocerata* | Protection Is, WA (1981) | *32.59 | 0.061 | 440 | **9.91** | **-0.085** | Wilson and Manuwal (1986) |
| *Fratercula cirrhata* | Okhotsk Sea (1994) | 20.41 | 0.118 | 621 | **19.17** | **-0.034** | Kitaysky (1999) |
| *Fratercula cirrhata* | Buldir Is, AK (1975) | *19.35 | 0.074 | 360 | **12.02** | **-0.090** | Wehle (1983) |
| *Fratercula cirrhata* | Ugaiushak Is, AK (1976) | *16.27 | 0.125 | 600 | **20.31** | **-0.040** | Wehle (1983) |
| *Fratercula cirrhata* | Barren Is, AK (1976) | *18.53 | 0.111 | 600 | **18.04** | **-0.045** | Wehle (1983) |
| *Fratercula cirrhata* | Chowiet Is, AK (1976) | *14.54 | 0.091 | 330 | **14.79** | **-0.077** | Wehle (1983) |
| *Fratercula cirrhata* | Shumagin Is, AK (1976) | *12.90 | 0.145 | 520 | **23.56** | **-0.038** | Wehle (1983) |
| *Fratercula cirrhata* | Wooded Is, AK (1976) | *16.13 | 0.120 | 550 | **19.50** | **-0.044** | Wehle (1983) |
| *Fratercula cirrhata* | Ugaiushak Is, AK (1977) | *12.72 | 0.153 | 555 | **24.86** | **-0.034** | Wehle (1983) |
| *Fratercula cirrhata* | Barren Is, AK (1977) | *18.62 | 0.110 | 595 | **17.87** | **-0.045** | Wehle (1983) |
| *Fratercula cirrhata* | Sitkalidak, AK (1977) | *15.88 | 0.126 | 590 | **20.47** | **-0.041** | Wehle (1983) |
| *Fratercula cirrhata* | Cathedral Is, AK (1977) | *15.71 | 0.127 | 580 | **20.64** | **-0.040** | Wehle (1983) |
| *Fratercula corniculata* | Buldir Is, AK (1975) | *20.13 | 0.075 | 300 | **12.18** | **-0.086** | Wehle (1983) |
| *Fratercula corniculata* | Barren Is, AK (1976) | *16.07 | 0.122 | 440 | **19.82** | **-0.043** | Wehle (1983) |
| *Fratercula corniculata* | Chowiet Is, AK (1976) | *12.61 | 0.113 | 280 | **18.36** | **-0.059** | Wehle (1983) |
| *Fratercula corniculata* | Shumagin Is, AK (1976) | *12.95 | 0.144 | 405 | **23.40** | **-0.038** | Wehle (1983) |
| *Fratercula corniculata* | Ugaiushak Is, AK (1977) | *12.89 | 0.139 | 380 | **22.59** | **-0.041** | Wehle (1983) |
| *Fratercula corniculata* | Barren Is, AK (1977) | *17.31 | 0.114 | 445 | **18.52** | **-0.046** | Wehle (1983) |
| **Hydrobatidae** | | | | | | | |
| *Oceanodroma homochroa* | Farallon Is, CA (1985) | *13.56 | 0.108 | 49 | **17.55** | **-0.061** | Ainley *et al.* (1990) |
| **Laridae** | | | | | | | |
| *Larus atricilla* | Florida (1972) | *13.45 | ¤0.162 | 310 | **26.32** | **-0.029** | Dinsmore and Schreiber (1974) |
| *Larus ridibundus* | The Netherlands (2000) | 9.90 | 0.200 | 237 | **32.50** | **-0.026** | Eising and Groothuis (2003) |
| *Sterna hirundo* | Great Gull Is, NY (1968) | 8.22 | 0.246 | 113 | **39.97** | **-0.021** | LeCroy and Collins (1972) |
| *Sterna paradisaea* | Shetland Is (1975) | 7.50 | 0.288 | 111 | **46.80** | **-0.016** | Furness (1978) |
| **Pelecanoididae** | | | | | | | |
| *Pelecanoides georgicus* | S Georgia (1982) | 14.90 | 0.145 | 148 | **23.56** | **-0.032** | Roby (1991) |
| *Pelecanoides urinatrix* | S Georgia (1982) | 15.60 | 0.146 | 139 | **23.72** | **-0.030** | Roby (1991) |
| **Phaethontidae** | | | | | | | |
| *Phaethon lepturus* | Seychelles (2002) | 35.00 | ¤0.155 | 362 | **25.19** | **0.027** | Ramos and Pacheco (2003) |

**Table 2** continued.

| Species | Area (Year) | $t_l$ | $K_l$ | $W_\infty$ | $K$ | $t_o$ | Source |
|---|---|---|---|---|---|---|---|
| **Spheniscidae** | | | | | | | |
| *Eudyptula minor* | Victoria, Australia (1980) | 20.00 | 0.104 | 951 | **16.90** | **-0.047** | Montague (1982) |
| | Victoria, Australia (1981) | 21.40 | 0.168 | 793 | **27.30** | **-0.004** | Montague (1982) |
| | Tasmania (1970) | 17.10 | 0.152 | 836 | **24.70** | **-0.023** | Hodgson (1975) |
| | New Zealand (1975) | 16.10 | 0.158 | 642 | **25.67** | **-0.023** | Jones (1978) |
| | New Zealand (1958) | 21.40 | 0.123 | 1110 | **19.99** | **-0.028** | Kinsky (1960) |
| | New Zealand (1938) | 18.10 | 0.122 | 1148 | **19.82** | **-0.037** | Richdale (1940) |
| | New Zealand (1983) | 19.60 | 0.125 | 1154 | **20.31** | **-0.031** | Gales (1987) |
| **Stercorariidae** | | | | | | | |
| *Catharacta skua* | Shetland Is. (1975) | 16.96 | 0.176 | 1167 | **28.60** | **-0.014** | Furness (1978) |

* Estimated using equation 2 described in the methodology.

¤ Estimated using equation 3 described in the methodology.

## RESULTS

Table 2 summarizes the logistic growth parameters as extracted from the corresponding studies, as well as the growth parameters we re-expressed using the VBGF. Similarly, Table 3 summarizes growth parameters derived from the Gompertz growth model, which we then re-expressed using the VBGF. Lastly, Table 4 summarizes VBGF parameters re-estimated after tracing and re-analyzing originally published weight-at-age data. $W_\infty$ values ranged from 36 g for the Wilson's storm petrel (*Oceanites oceanicus*) chicks (Table 4), to 15,243 g for the Wandering albatross (*Diomedea exulans*) chicks both from the Crozet Islands, Southern Ocean (Table 4).

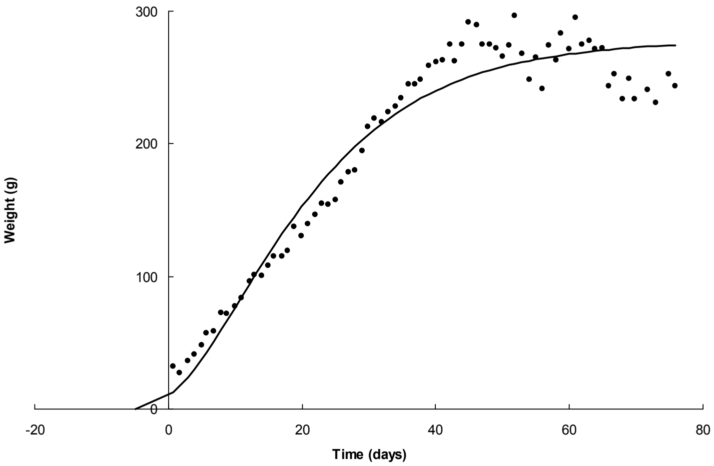

**Figure 2.** Von Bertalanffy growth function (solid line) for Little shearwater (*Puffinus assimilis*) chicks from Lady Alice Island, New Zealand, re-estimated using original weight-at-age data (black dot) published by Booth *et al.* (2000).

The most intensively studied species were the Pigeon guillemot (*Cepphus columba*), the Rhinoceros auklet (*Cerorhinca monocerata*), the Atlantic puffin (*Fratercula arctica*), the Tufted puffin (*Fratercula cirrhata*), the Horned puffin (*Fratercula corniculata*), the Common tern (*Sterna hirundo*), the Black-legged kittiwake (*Rissa tridactyla*), the Thick-billed murre (*Uria lomvia*), and the Blue penguin (*Eudyptula minor*). They were represented by more than 10 seabird populations each (Tables 2 to 4), and comprised 31% of all seabird populations compiled (138 out of 447; Tables 2 to 4). All the above-mentioned seabird species, with the exception of the Blue penguin, belong to the order Charadriiformes (Tables 2 to 4).

$K_L$ values ranged from 0.049 days$^{-1}$ for the Rhinoceros auklet chicks of Destruction Island, off the coast of Washington State (Table 2), to 0.288 days$^{-1}$ for the Arctic tern (*Sterna paradisaea*) chicks of Shetland Islands, UK (Table 2). $K_L$ values were not available for nine seabird populations (Table 2). These were estimated using equation 2 described above. The values of $t_L$ ranged from 7.5 days for the Arctic tern chicks of Shetland Islands, UK (Table 2), to 39.5 days for the Rhinoceros auklet chicks of Destruction Island, off the coast of Washington State (Table 2). Values of $t_L$ were lacking for 35 seabird populations (Table 2). These were estimated using equation 3 described in the methodology section.

**Table 3.** Growth parameters of seabird chicks from the Gompertz growth curve (in normal font), and also estimated for this paper (in bold), using the von Bertalanffy growth function (VBGF). $W_\infty$ (in g): the asymptotic weight of chicks for both the Gompertz curve and VBGF; $t_G$ (in days) and $K_G$ (in days$^{-1}$): the inflection point and the growth constant for the Gompertz curve respectively; $t_o$ (in years) and $K$ (in years$^{-1}$): the hypothetical 'age' chicks would have at zero weight and the growth constant for VBGF respectively. AK: Alaska.

| Species | Area (Year) | $t_G$ | $K_G$ | $W_\infty$ | $K$ | $t_o$ | Source |
|---|---|---|---|---|---|---|---|
| **Diomedeidae** | | | | | | | |
| *Phoebastria immutabilis* | Hawaii (1987) | 19.00 | 0.050 | 2836 | **14.84** | **-0.037** | Sievert and Sileo (1993) |
| *Phoebastria nigripes* | Hawaii (1987) | 17.90 | 0.056 | 2714 | **16.62** | **-0.010** | Sievert and Sileo (1993) |
| *Phoebetria palpebrata* | Macquarie Is (2000) | 32.40 | 0.047 | 4760 | **13.95** | **-0.006** | Terauds and Gales (2006) |

$K_G$ values ranged from 0.047 days$^{-1}$ for the Light-mantled albatross (*Phoebetria palpebrata*) chicks of Macquarie Island, Southern Ocean (Table 3), to 0.056 days$^{-1}$ for the Black-footed albatross (*Phoebastria nigripes*) chicks of Hawaii (Table 3). In addition, $t_G$ ranged from 17.9 days for the Black-footed albatross chicks of Hawaii (Table 3), to 32.4 days for the Light-mantled albatross chicks of Macquarie Island, Southern Ocean (Table 3).

When re-expressed through VBGF, the logistic growth curve deviated from VBGF by 13%, while the Gompertz curve deviated by only 3%. This suggests that the VBGF and the Gompertz curves are equivalent.

Computed $K$ values ranged from 3.22 years$^{-1}$ for the Wandering albatross chicks of the Crozet Islands, Southern Ocean (Table A1), to 61.46 years$^{-1}$ for the Cory's shearwater (*Calonectris diomedea*) chicks of Selvagem Grande, of the Madeira archipelago (Table A1). Moreover, $t_o$ values ranged from -0.111 years for the Rhinoceros auklet chicks of Destruction Island, off the coast of Washington State (Table 2), to -0.001 years for the Whiskered auklet (*Aethia pygmaea*) chicks of Buldir Island, Alaska (Table A1), the Rhinoceros auklet chicks of Teuri Island, Japan (Table A1), and the Masked booby (*Sula dactylatra*) chicks, of Kure Atoll, Hawaii (Table A1).

**Table 4.** Regression equations between the von Bertalanffy growth parameters $K$ and $W_\infty$, for four orders and all seabird species combined. SE(b): Standard error of the slope. r: The correlation coefficient. N: The number of seabird populations representing each order. All regressions were statistically significant ($P<0.05$).

| Order | Regression | SE(b) | r | N | P |
|---|---|---|---|---|---|
| Charadriiformes | $\mathrm{Log}K=2.18-0.31\mathrm{Log}W_\infty$ | 0.03 | -0.53 | 239 | $P<0.05$ |
| Pelecaniformes | $\mathrm{Log}K=1.63-0.12\mathrm{Log}W_\infty$ | 0.05 | -0.35 | 50 | $P<0.05$ |
| Procellariiformes | $\mathrm{Log}K=1.79-0.18\mathrm{Log}W_\infty$ | 0.02 | -0.61 | 111 | $P<0.05$ |
| Sphenisciformes | $\mathrm{Log}K=2.35-0.32\mathrm{Log}W_\infty$ | 0.05 | -0.70 | 47 | $P<0.05$ |
| All seabirds | $\mathrm{Log}K=1.93-0.21\mathrm{Log}W_\infty$ | 0.01 | -0.62 | 445 | $P<0.05$ |

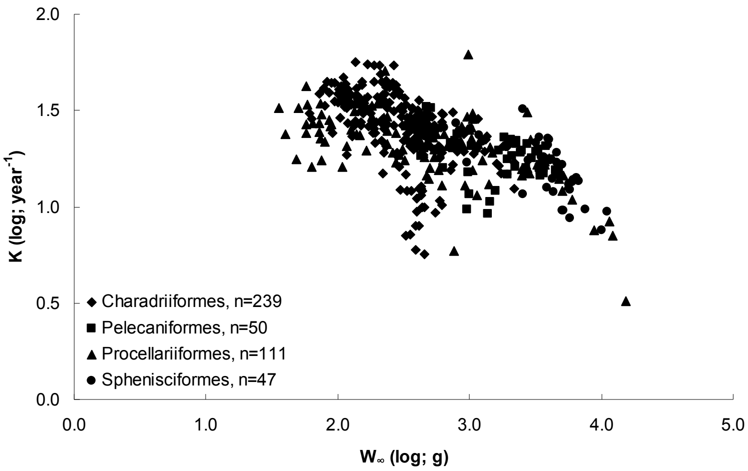

**Figure 3.** Auximetric plot for the four orders of Charadriiformes, Sphenisciformes, Procellariiformes and Pelecaniformes (see text).

A negative relationship between the logarithmic values of $W_\infty$ and $K$ was identified for the orders of Charadriiformes, Pelecaniformes, Procellariiformes, and Sphenisciformes as well as for all seabird species combined (Table 4, Figure 3). Each order was represented by 239, 50, 111 and 47 seabird populations respectively (Table 4, Figure 3). The values of the slope ranged from -0.32 for Sphenisciformes, to -0.12 for Pelecaniformes (Table 4). All regressions were statistically significant ($P<0.05$; Table 4). This justifies the use of auximetric plots in seabirds.

## DISCUSSION

In the present study, relationships were established between the life-history parameters $K$ and $W_\infty$, for a number of seabird populations around the globe. However, these relationships were based on information available for about 39% of the world's seabirds (137 out of 351 in Karpouzi *et al.*, 2007). Thus, these relationships are provisional and subject to change when additional information becomes available. Nonetheless, they can be particularly useful in estimating approximate values of K from $W_\infty$, and hence to obtain a preliminary growth curve for species without growth data. In addition, they allow us to compare growth patterns of seabirds to those from other groups of organisms, whose growth has also been described using the VBGF.

Similar studies that investigate the relationship between the growth parameters $K$ and asymptotic size have also been conducted mainly for fish species of marine and freshwater ecosystems. In particular, Winemiller and Rose (1992) analyzed life-history patterns of 216 North American marine and freshwater fish species, belonging to 57 families. Pauly (1998) analyzed growth parameters for 4826 fish populations listed in FishBase (www.fishbase.org; Froese and Pauly, 2000). Stergiou (2000) explored life-history patterns for 40 fish species from Greek waters, belonging to 20 families, and compared them with those from Pauly (1998).

Starck and Ricklefs (1998) compiled information on the growth parameters $K_L$, $K_G$ and $W_\infty$ for 1117 populations, belonging to 557 bird species, from both terrestrial and aquatic ecosystems. Out of these, 366 belonged to marine birds and represented 114 seabird species, and 13 families (Starck and Ricklefs, 1998). Ricklefs *et al.* (1998) and later Visser (2002) used these data to examine the relationship between $K_L$ and $W_\infty$. Their analyses revealed that growth rates are particularly low for many pelagic seabird species, and tend to be higher in species that feed close to shore, such as the larid species. In addition, highest growth rates are observed among penguin species (Ricklefs *et al.*, 1998; Visser, 2002).

The VBGF parameters can be linked by the relation $W_\infty=a*K^{-b}$ (e.g., Beverton and Holt, 1959; Adams, 1980; Pauly, 1980; Charnov, 1993; Pauly, 1998; Froese and Pauly, 2000). For fish, the exponent b takes values that generally range from -0.27 to -0.80 (Charnov, 1993; Stergiou, 2000). The value of $b$ for all Greek fish stocks is equal to -0.32 (Stergiou, 2000). In contrast, the value of $b$ equals -0.57 for the 4826 populations analyzed by Pauly (1998). When all seabird populations were taken into account, the slope on the auximetric plot was equal to -0.21 (Table 5). This value was heavily influenced by 53% of the $K$ and $W_\infty$ values of Charadriiformes (239 out of 447 seabird populations; Table 5). Hence, it may be subject to change when growth parameter estimates from other seabird species belonging to the other three orders becomes available.

The auximetric plot revealed differences in the growth potential of the seabird species included in this study (Figure 3). Indeed, the growth spaces occupied by the four orders of seabirds seem to reflect differences in the seabirds' breeding biology (e.g., adult foraging behaviour during chick-rearing; e.g., Fernández *et al.*, 2001; parental feeding strategies; e.g., Ydenberg, 1989). In particular, tern and gull species with generally smaller body size exhibited faster growth rates (Figure 3). These are species that produce large clutches, which tend to transport food from areas close to shore to feed their young (e.g., Hulsman and Smith, 1988). On the other hand, alcid species, also characterized by small body size, grow more slowly (Figure 3). Alcid species produce single-egg clutches, and exhibit a more pelagic, nocturnal foraging behaviour (e.g., Sealy, 1973; Ricklefs, 1982, 1990). As a result, provisioning rates, and consequently growth rates of chicks, are reduced (e.g., Sealy, 1973; Ricklefs, 1982, 1990).

Some procellariiform species (e.g., storm petrels of the family Hydrobatidae) also displayed a growth pattern similar to that of the alcid species (Table 4; Figure 3). Storm petrels are small in size. However, the growth rates of their chicks are relatively low (Table 4; Figure 3). Storm petrels feed far from nesting colonies on prey that is sparse and unpredictably distributed. The single-clutch size may suggest that their ability to deliver energy to the brood is severely limited (e.g., Place *et al.*, 1989). Slow growth may be an adaptation to reduce the rate at which chicks require energy for development, thus making it easier for parents to utilize more distant and sparse food resources for breeding (e.g., Ricklefs *et al.*, 1980; Place *et al.*, 1989).

The large-bodied Sphenisciformes (i.e., penguins) exhibited high growth rates (Tables 2 and 4; Figure 3). A similar growth pattern was also observed by Visser (2002). This has been interpreted as an adaptation to the severe Antarctic conditions that shorten the breeding season. Indeed, faster growth rates enable chicks to leave the colony before the beginning of the winter (Volkman and Trivelpiece, 1980; Visser, 2002). Lastly, albatross species with large body size exhibited slow growth rates (Tables 3 and 4; Figure 3). This growth pattern is typical of the albatross family, which is dominated by long-distance foragers (e.g., Fernández *et al.*, 2001). Albatross chicks require nine to ten months to develop to adult body size at fledging (e.g., Berrow *et al.*, 1999; Mabille *et al.*, 2004). Thus, developmental period spans the winter season, and chicks must endure severe winter conditions and variability in parental provisioning efforts (e.g., Berrow *et al.*, 1999; Mabille *et al.*, 2004).

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**Table A1**. Growth parameters of seabird chicks re-estimated for this paper using the von Bertalanffy growth function (VBGF), from body weight-at-age data published in the original studies. $W_\infty$ (g): the asymptotic weight of chicks; $K$ (years$^{-1}$) and $t_o$ (in years): the growth constant and the hypothetical 'age' chicks would have at zero weight respectively.

| Species | Area (Year) | $W_\infty$ | $K$ | $t_o$ | Source |
|---|---|---|---|---|---|
| **Alcidae** | | | | | |
| *Aethia cristatella* | Buldir Is, Alaska (1996) | 376 | 20.47 | -0.011 | Fraser *et al.* (1999) |
| | Buldir Is, Alaska (1997) | 358 | 20.62 | -0.011 | Fraser *et al.* (1999) |
| | St Lawrence Is, Alaska (1987) | 299 | 32.75 | -0.018 | Piatt *et al.* (1990) |
| *Aethia pusilla* | Kiska Is, Alaska (2003) | 80 | 33.60 | -0.018 | Major *et al.* (2006) |
| | Pribilof Is, Alaska (1982) | 114 | 34.41 | -0.018 | Roby and Brink (1986) |
| | St Lawrence Is, Alaska (1987) | 95 | 35.40 | -0.019 | Piatt *et al.* (1990) |
| *Aethia pygmaea* | Buldir Is Alaska (1998) | 113 | 32.92 | -0.018 | Hunter *et al.* (2002) |
| *Alca torda* | Machias Seal Is (1995) | 189 | 44.81 | -0.022 | Bond *et al.* (2006) |
| | Machias Seal Is (2003) | 208 | 54.25 | -0.022 | Bond *et al.* (2006) |
| *Alle alle* | Franz Josef Land (1993) | 152 | 44.37 | -0.021 | Stempniewicz *et al.* (1996) |
| | Svalbard (1978) | 138 | 41.05 | -0.015 | Clark and Ydenberg (1990) |
| | Svalbard (1984) | 136 | 37.53 | -0.019 | Clark and Ydenberg (1990) |
| | Svalbard (1987) | 178 | 30.53 | -0.019 | Konarzewski and Taylor (1989) |
| | Svalbard (1992) | 138 | 37.80 | -0.019 | Stempniewicz *et al.* (1996) |
| *Brachyramphus marmoratus* | Barren Is, Alaska (1978) | 152 | 42.84 | -0.021 | Simons (1980) |
| | Barren Is, Alaska (1979) | 167 | 37.16 | -0.020 | Hirsch *et al.* (1981) |
| *Cepphus carbo* | Teuri Is, Japan (1989) | 806 | 19.45 | -0.017 | Minami *et al.* (1995) |
| *Cepphus columba* | Farallon Is, California (1985) | 447 | 28.59 | -0.016 | Ainley and Boekelheide (1990) |
| | Mandarte Is, British Columbia (1960) | 476 | 27.19 | -0.017 | Drent (1965) |
| | Mitlenatch Is, British Columbia (1985) | 421 | 29.61 | -0.015 | Emms and Verbeek (1991) |
| | Prince William Sound, Alaska (1978) | 607 | 26.04 | -0.015 | Oakley (1981) |
| | Queen Charlotte Is, British Columbia (1991) | 412 | 29.82 | -0.016 | Vermeer *et al.* (1993) |
| *Cepphus grylle* | Piqiuliit, Nunavut (1983) | 404 | 28.10 | -0.016 | Cairns (1987) |
| | Pitsiulak, Nunavut (1981) | 386 | 28.53 | -0.017 | Cairns (1987) |
| | Pitsiulak, Nunavut (1982) | 408 | 26.76 | -0.018 | Cairns (1987) |
| | Pitsiulak, Nunavut (1983) | 447 | 26.09 | -0.017 | Cairns (1987) |
| | Québec (1977) | 448 | 25.60 | -0.018 | Cairns (1981) |
| *Cerorhinca monocerata* | Cleland Is, British Columbia (1969) | 455 | 10.00 | -0.054 | Summers and Drent (1979) |
| | Protection Is, Washington (1989) | 355 | 7.15 | -0.076 | Wilson (1993) |
| | Protection Is, Washington (1990) | 392 | 6.01 | -0.091 | Wilson (1993) |
| | Protection Is, Washington (1991) | 455 | 5.69 | -0.104 | Wilson (1993) |
| | Teuri Is, Japan (1994) | 593 | 10.78 | -0.005 | Takahashi *et al.* (2001) |
| | Teuri Is, Japan (1995) | 615 | 10.20 | -0.001 | Takahashi *et al.* (2001) |
| | Teuri Is, Japan (1996) | 550 | 9.35 | -0.006 | Takahashi *et al.* (2001) |
| | Teuri Is, Japan (1997) | 329 | 7.10 | -0.072 | Takahashi *et al.* (2001) |
| | Teuri Is, Japan (1998) | 439 | 12.07 | -0.004 | Takahashi *et al.* (2001) |
| | Triangle Is, British Columbia (1978) | 406 | 22.04 | -0.026 | Vermeer and Cullen (1982) |
| *Cyclorrhynchus psittacula* | Buldir Is, Alaska (1991) | 266 | 26.47 | -0.017 | Hipfner and Byrd (1993) |

**Appendix 1**. Continued

| **Species** | **Area (Year)** | $W_\infty$ | $K$ | $t_o$ | **Source** |
|---|---|---|---|---|---|
| *Fratercula arctica* | Bleiksøy, Norway (1982) | 280 | 19.00 | -0.039 | Barrett *et al.* (1987) |
| | Bleiksøy, Norway (1986) | 118 | 36.54 | -0.030 | Barrett and Rikardsen (1992) |
| | Bleiksøy, Norway (1987) | 221 | 14.86 | -0.053 | Barrett and Rikardsen (1992) |
| | Farne Is, UK (1963) | 195 | 27.51 | -0.028 | Pearson (1968) |
| | Gannet Is, Newfoundland (1996) | 317 | 22.11 | -0.028 | Baillie and Jones (2003) |
| | Gannet Is, Newfoundland (1997) | 442 | 18.01 | -0.032 | Baillie and Jones (2003) |
| | Gannet Is, Newfoundland (1998) | 438 | 20.00 | -0.029 | Baillie and Jones (2003) |
| | Gull Is, Newfoundland (1998) | 236 | 26.61 | -0.028 | Baillie and Jones (2003) |
| | Hornøy, Norway (1980) | 387 | 29.49 | -0.018 | Barrett *et al.* (1987) |
| | Hornøy, Norway (1981) | 372 | 32.72 | -0.020 | Barrett and Rikardsen (1992) |
| | Is May, UK (1975) | 334 | 28.87 | -0.018 | Harris (1978) |
| | Is May, UK (1992) | 265 | 31.23 | -0.024 | Wernham and Bryant (1998) |
| | Is May, UK (1995) | 310 | 31.28 | -0.019 | Cook and Hamer (1997) |
| | Machias Seal Is (1997) | 367 | 26.58 | -0.019 | Bond *et al.* (2006) |
| | Machias Seal Is (1999) | 221 | 28.49 | -0.029 | Bond *et al.* (2006) |
| | Machias Seal Is (2003) | 379 | 19.74 | -0.029 | Bond *et al.* (2006) |
| | Røst, Norway (1983) | 377 | 27.15 | -0.017 | Barrett *et al.* (1987) |
| | Røst, Norway (1984) | 222 | 35.49 | -0.020 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1985) | 292 | 16.10 | -0.040 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1988) | 182 | 26.37 | -0.030 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1989) | 326 | 33.76 | -0.019 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1990) | 304 | 31.81 | -0.018 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1991) | 306 | 29.50 | -0.018 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1992) | 368 | 32.27 | -0.018 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1993) | 228 | 43.54 | -0.019 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1996) | 219 | 37.92 | -0.021 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (1999) | 260 | 43.68 | -0.020 | Anker-Nilssen and Aarvak (2002) |
| | Røst, Norway (2000) | 188 | 53.82 | -0.022 | Anker-Nilssen and Aarvak (2002) |
| | W Scotland, UK (1975) | 339 | 21.81 | -0.025 | Harris (1978) |
| | Wales, UK (1977) | 353 | 27.07 | -0.016 | Ashcroft (1979) |
| | Wales, UK (1978) | 337 | 23.81 | -0.017 | Hudson (1979) |
| *Fratercula cirrhata* | Destruction Is, Washington (1975) | 528 | 25.50 | -0.017 | Burrell (1980) |
| | Prince William Sound, Alaska (1995) | 604 | 25.82 | -0.017 | Piatt *et al.* (1997) |
| | Triangle Is, British Columbia (2000) | 517 | 29.38 | -0.027 | Gjerdrum (2004) |
| *Fratercula corniculata* | Duck Is, Alaska (1995) | 511 | 20.31 | -0.033 | Harding *et al.* (2003) |
| | Duck Is, Alaska (1996) | 371 | 26.23 | -0.025 | Harding *et al.* (2003) |
| | Duck Is, Alaska (1997) | 472 | 20.43 | -0.039 | Harding *et al.* (2003) |
| | Duck Is, Alaska (1998) | 303 | 33.01 | -0.026 | Harding *et al.* (2003) |
| | Duck Is, Alaska (1999) | 402 | 31.80 | -0.021 | Harding *et al.* (2003) |

**Appendix 1**. Continued

| **Species** | **Area (Year)** | $W_\infty$ | $K$ | $t_o$ | **Source** |
|---|---|---|---|---|---|
| *Ptychoramphus aleuticus* | California Channel Is (2001) | 150 | 26.45 | -0.027 | Ackerman *et al.* (2004) |
| | California (1959) | 155 | 30.42 | -0.016 | Thoresen (1964) |
| | Farallon Is, California (1971) | 192 | 21.59 | -0.014 | Manuwal (1974) |
| | Triangle Is, British Columbia (1996) | 118 | 32.70 | -0.018 | Hedd *et al.* (2002a) |
| | Triangle Is, British Columbia (1997) | 149 | 31.15 | -0.018 | Hedd *et al.* (2002a) |
| | Triangle Is, British Columbia (1998) | 136 | 27.99 | -0.021 | Hedd *et al.* (2002a) |
| | Triangle Is, British Columbia (1999) | 187 | 25.48 | -0.019 | Hedd *et al.* (2002a) |
| *Uria aalge* | Farne Is, UK (1963) | 169 | 55.21 | -0.023 | Pearson (1968) |
| | Is May, UK (1992) | 267 | 54.34 | -0.022 | Harris and Wanless (1995) |
| | St Lawrence Is, Alaska (1972) | 229 | 38.73 | -0.026 | Johnson and West (1975) |
| | Sweden (1974) | 320 | 36.74 | -0.021 | Hedgren and Linnman (1979) |
| | Sweden (1975) | 278 | 43.02 | -0.021 | Hedgren and Linnman (1979) |
| | Sweden (1976) | 291 | 37.97 | -0.022 | Hedgren and Linnman (1979) |
| | Sweden (1977) | 292 | 39.64 | -0.021 | Hedgren and Linnman (1979) |
| | Wales, UK (1987) | 234 | 45.19 | -0.022 | Hatchwell (1991) |
| *Uria lomvia* | Cape Hay, Northwest Territories (1979) | 215 | 44.67 | -0.021 | Birkhead and Nettleship (1981) |
| | Coats Is, Nunavut (1991) | 268 | 41.66 | -0.021 | de Forest and Gaston (1996) |
| | Coats Is, Nunavut (1994) | 268 | 37.92 | -0.024 | Hipfner *et al.* (2006) |
| | Coats Is, Nunavut (1995) | 231 | 41.69 | -0.023 | Hipfner *et al.* (2006) |
| | Coburg Is, Northwest Territories (1979) | 247 | 41.48 | -0.021 | Birkhead and Nettleship (1981) |
| | Digges Is, Nunavut (1999) | 137 | 56.41 | -0.023 | Hipfner *et al.* (2006) |
| | Prince Leopold Is, Nunavut (2000) | 305 | 33.09 | -0.019 | Gaston *et al.* (2005) |
| | Prince Leopold Is, Nunavut (2001) | 200 | 36.92 | -0.021 | Gaston *et al.* (2005) |
| | Prince Leopold Is, Nunavut (2002) | 117 | 41.05 | -0.024 | Gaston *et al.* (2005) |
| | St Lawrence Is, Alaska (1972) | 211 | 48.51 | -0.023 | Johnson and West (1975) |
| **Diomedeidae** | | | | | |
| *Diomedea amsterdamensis* | Amsterdam Is (1984) | 8818 | 7.58 | -0.028 | Jouventin *et al.* (1989) |
| *Diomedea exulans* | Crozet Is (1986) | 12249 | 7.06 | -0.033 | Lequette and Weimerskirch (1990) |
| | Crozet Is (1994) | 11557 | 8.35 | -0.038 | Weimerskirch and Lys (2000) |
| | Crozet Is (2000) | 15243 | 3.22 | -0.006 | Mabille *et al.* (2004) |
| *Phoebastria immutabilis* | Midway Atoll, Hawaii (1965) | 2478 | 15.72 | -0.037 | Fisher (1967) |
| *Phoebetria palpebrata* | Macquarie Is (2001) | 3741 | 16.58 | -0.011 | Terauds and Gales (2006) |
| | S Georgia (1977) | 3247 | 16.46 | -0.017 | Thomas *et al.* (1983) |
| *Thalassarche cauta* | Albatross Is, Australia (1998) | 5986 | 10.84 | -0.060 | Hedd *et al.* (2002b) |
| *Thalassarche chlororhynchos* | Amsterdam Is (1996) | 2921 | 22.29 | -0.041 | Weimerskirch *et al.* (2001) |
| | Amsterdam Is (1997) | 2492 | 14.42 | -0.086 | Weimerskirch *et al.* (2001) |
| | Amsterdam Is (2001) | 2732 | 31.01 | -0.029 | Pinaud *et al.* (2005) |
| *Thalassarche chrysostoma* | S Georgia (1976) | 5090 | 12.02 | -0.025 | Ricketts and Prince (1981) |
| | S Georgia (1996) | 3755 | 17.18 | -0.003 | Huin and Prince (2000) |
| *Thalassarche melanophris* | S Georgia (1976) | 5540 | 12.92 | -0.023 | Ricketts and Prince (1981) |
| | S Georgia (1996) | 4002 | 17.93 | -0.006 | Huin and Prince (2000) |
| **Fregatidae** | | | | | |
| *Fregata magnificens* | Baja California, Mexico (1988) | 1424 | 10.58 | -0.021 | Carmona *et al.* (1995) |
| | Barbuda (1971) | 1369 | 9.15 | -0.042 | Diamond (1973) |

**Appendix 1**. Continued

| Species | Area (Year) | $W_\infty$ | $K$ | $t_o$ | Source |
|---|---|---|---|---|---|
| **Hydrobatidae** | | | | | |
| *Fregetta tropica* | Crozet Is (1982) | 50 | 32.70 | -0.023 | Jouventin *et al*. (1985) |
| | S Shetland Is (1996) | 118 | 20.74 | -0.022 | Hahn (1998) |
| *Garrodia nereis* | Chatham Is, New Zealand (1987) | 74 | 22.53 | -0.019 | Plant (1989) |
| *Hydrobates pelagicus* | Shetland Is, UK (1992) | 40 | 23.69 | -0.024 | Bolton (1995) |
| *Oceanites oceanicus* | Crozet Is (1982) | 36 | 32.36 | -0.023 | Jouventin *et al*. (1985) |
| | S Shetland Is (1996) | 59 | 33.99 | -0.017 | Quillfeldt and Peter (2000) |
| | W Antarctic Peninsula (1986) | 58 | 26.92 | -0.025 | Obst and Nagy (1993) |
| *Oceanodroma furcata* | Barren Is, Alaska (1976) | 87 | 26.24 | -0.021 | Boersma *et al*. (1980) |
| | Barren Is, Alaska (1977) | 80 | 21.67 | -0.028 | Boersma *et al*. (1980) |
| | Barren Is, Alaska (1978) | 86 | 28.28 | -0.018 | Simons (1981) |
| | Queen Charlotte Is, British Columbia (1983) | 76 | 30.29 | -0.020 | Vermeer *et al*. (1988) |
| *Oceanodroma leucorhoa* | Kent Is, New Brunswick (1962) | 73 | 27.30 | -0.018 | Ricklefs *et al*. (1985) |
| | Kent Is, New Brunswick (1972) | 58 | 24.26 | -0.023 | Ricklefs *et al*. (1980) |
| | Kent Is, New Brunswick (1983) | 72 | 24.29 | -0.022 | Ricklefs *et al*. (1985) |
| | Kent Is, New Brunswick (1988) | 76 | 17.50 | -0.041 | Ricklefs and Schew (1994) |
| | Queen Charlotte Is, British Columbia (1983) | 65 | 27.30 | -0.020 | Vermeer *et al*. (1988) |
| *Oceanodroma tristrami* | Laysan Is, Hawaii (1991) | 90 | 26.89 | -0.009 | Marks and Leasure (1992) |
| *Pelagodroma marina* | Selvagem Grande (1996) | 58 | 42.52 | -0.019 | Campos and Granadeiro (1999) |
| | Victoria, Australia (2003) | 74 | 34.22 | -0.017 | Underwood and Bunce (2004) |
| | Victoria, Australia (2003) | 63 | 16.12 | -0.042 | Underwood and Bunce (2004) |
| **Laridae** | | | | | |
| *Anous minutus* | Hawaii (1981) | 117 | 33.44 | -0.019 | Pettit *et al*. (1984a) |
| *Anous stolidus* | Manana Is, Hawaii (1972) | 171 | 31.73 | -0.018 | Brown (1976a) |
| | Puerto Rico (1989) | 180 | 33.19 | -0.018 | Morris and Chardine (1992) |
| | Seychelles (1995) | 214 | 21.94 | -0.027 | Ramos *et al*. (2006) |
| | Seychelles (1996) | 187 | 27.39 | -0.017 | Ramos *et al*. (2006) |
| | Seychelles (2001) | 226 | 19.06 | -0.020 | Ramos *et al*. (2006) |
| | Tern Is, Hawaii (1989) | 222 | 25.36 | -0.024 | Megyesi and Griffin (1996) |
| *Anous tenuirostris* | Houtman Abrolhos, Australia (1991) | 110 | 34.26 | -0.020 | Surman and Wooller (1995) |
| | Seychelles (1995) | 100 | 34.61 | -0.019 | Ramos *et al*. (2006) |
| | Seychelles (1996) | 106 | 37.33 | -0.019 | Ramos *et al*. (2006) |
| | Seychelles (1997) | 104 | 28.84 | -0.026 | Ramos *et al*. (2006) |
| | Seychelles (2001) | 100 | 38.66 | -0.019 | Ramos *et al*. (2006) |
| | Seychelles (2002) | 83 | 44.31 | -0.019 | Ramos *et al*. (2006) |
| *Chlidonias niger* | The Netherlands (1995) | 78 | 41.13 | -0.019 | Beintema (1997) |
| *Creagrus furcatus* | Galápagos (1966) | 701 | 20.37 | -0.015 | Harris (1970a) |
| | Galápagos (1967) | 752 | 16.55 | -0.027 | Harris (1970a) |
| *Gygis alba* | Hawaii (1981) | 117 | 18.58 | -0.021 | Pettit *et al*. (1984a) |
| *Larus argentatus* | Appledore Is, New Hampshire (1973) | 1084 | 18.87 | -0.017 | Dunn and Brisbin (1980) |
| | Germany (1996) | 746 | 30.91 | -0.012 | Wilkens and Exo (1998) |
| *Larus atricilla* | Florida (1976) | 353 | 25.89 | -0.017 | Schreiber and Schreiber (1980) |

**Appendix 1**. Continued

| Species | Area (Year) | $W_\infty$ | $K$ | $t_o$ | Source |
|---|---|---|---|---|---|
| *Larus audouini* | Columbretes Is, Spain (2000) | 620 | 30.40 | -0.007 | Villuendas and Sarzo (2003) |
| | Turkey (1974) | 743 | 21.24 | -0.018 | Witt (1977) |
| *Larus californicus* | California (1986) | 897 | 19.40 | -0.010 | Jehl *et al*. (1990) |
| *Larus fuscus* | Farne Is, UK (1963) | 717 | 15.56 | -0.030 | Pearson (1968) |
| *Larus glaucescens* | Mandarte Is, British Columbia (1978) | 1308 | 19.38 | -0.013 | Verbeek and Morgan (1980) |
| | Squab Is, Alaska (1979) | 1326 | 22.25 | -0.017 | Murphy *et al*. (1984) |
| | Squab Is, Alaska (1980) | 2189 | 12.43 | -0.026 | Murphy *et al*. (1984) |
| *Larus modestus* | Chile (1986) | 302 | 19.11 | -0.005 | Guerra *et al*. (1988) |
| *Larus occidentalis* | Farallon Is, California (1970) | 902 | 23.70 | -0.016 | Coulter (1979) |
| | San Nicolas Is, California (1968) | 904 | 24.65 | -0.016 | Schreiber (1970) |
| *Larus ridibundus* | Germany (1986) | 325 | 26.58 | -0.018 | Nelsen and Brandl (1987) |
| | The Netherlands (2002) | 395 | 20.28 | -0.023 | Müller *et al*. (2005) |
| *Larus schistisagus* | Teuri Is, Japan (1984) | 1612 | 16.67 | -0.015 | Watanuki (1992) |
| | Teuri Is, Japan (1985) | 1668 | 16.38 | -0.013 | Watanuki (1992) |
| *Procelsterna cerulea* | Nihoa Is, Hawaii (1981) | 63 | 28.54 | -0.008 | Rauzon *et al*. (1984) |
| *Rissa brevirostris* | St George Is, Alaska (1993) | 422 | 29.68 | -0.018 | Lance and Roby (2000) |
| *Rissa tridactyla* | Bleiksøy, Norway (1986) | 503 | 24.97 | -0.017 | Barrett (1989) |
| | Farne Is, UK (1963) | 218 | 35.00 | -0.020 | Pearson (1968) |
| | Middleton Is, Alaska (1996) | 402 | 31.26 | -0.018 | Gill *et al*. (2002) |
| | Middleton Is, Alaska (1997) | 430 | 25.53 | -0.023 | Gill *et al*. (2002) |
| | Newfoundland (1970) | 415 | 35.85 | -0.018 | Maunder and Threlfall (1972) |
| | Norway (1973) | 518 | 25.50 | -0.018 | Barrett and Runde (1980) |
| | Norway (1974) | 474 | 30.58 | -0.017 | Barrett and Runde (1980) |
| | Norway (1976) | 476 | 30.90 | -0.018 | Barrett and Runde (1980) |
| | Prince William Sound, Alaska (1996) | 497 | 29.46 | -0.017 | Suryan *et al*. (2002) |
| | Prince William Sound, Alaska (1997) | 534 | 25.96 | -0.016 | Suryan *et al*. (2002) |
| | Prince William Sound, Alaska (1998) | 451 | 28.70 | -0.018 | Suryan *et al*. (2002) |
| | Prince William Sound, Alaska (1999) | 459 | 30.08 | -0.017 | Suryan *et al*. (2002) |
| | St George Is, Alaska (1993) | 544 | 26.44 | -0.017 | Lance and Roby (2000) |
| *Sterna albifrons* | Portugal (2003) | 61 | 30.60 | -0.018 | Paiva *et al*. (2006) |
| *Sterna anaethetus* | Great Barrier Reef (1980) | 128 | 23.08 | -0.031 | Hulsman and Langham (1985) |
| | Penguin Is, Australia (1990) | 119 | 27.28 | -0.024 | Garavanta and Wooller (2000) |
| *Sterna caspia* | California (1978) | 624 | 30.25 | -0.015 | Schew *et al*. (1994) |
| | New Zealand (1993) | 622 | 27.58 | -0.018 | Barlow and Dowding (2002) |
| *Sterna dougallii* | Great Barrier Reef (1986) | 92 | 24.12 | -0.029 | Milton *et al*. (1996) |
| | Rhode Is (1967) | 124 | 34.79 | -0.018 | LeCroy and Collins (1972) |
| | Rhode Is Sound (1990) | 107 | 42.46 | -0.018 | Nisbet *et al*. (1995) |
| *Sterna elegans* | California (1999) | 221 | 26.67 | -0.020 | Dahdul and Horn (2003) |
| *Sterna fuscata* | Hawaii (1972) | 193 | 24.01 | -0.025 | Brown (1976b) |

**Appendix 1**. Continued

| Species | Area (Year) | $W_\infty$ | $K$ | $t_o$ | Source |
|---|---|---|---|---|---|
| *Sterna hirundo* | Bird Is, Massachusetts (1999) | 136 | 37.74 | -0.019 | Apanius and Nisbet (2006) |
| | Couquet Is, UK (1966) | 181 | 27.70 | -0.017 | Langham (1972) |
| | Farne Is, UK (1963) | 86 | 38.96 | -0.021 | Pearson (1968) |
| | Germany (1999) | 150 | 33.83 | -0.019 | Becker and Wink (2003) |
| | Machias Seal Is (1995) | 149 | 31.18 | -0.018 | Bond *et al.* (2006) |
| | Machias Seal Is (1996) | 185 | 23.99 | -0.017 | Bond *et al.* (2006) |
| | Machias Seal Is (1997) | 127 | 33.96 | -0.019 | Bond *et al.* (2006) |
| | Machias Seal Is (1999) | 142 | 36.34 | -0.018 | Bond *et al.* (2006) |
| | Machias Seal Is (2000) | 125 | 34.90 | -0.019 | Bond *et al.* (2006) |
| | Machias Seal Is (2001) | 109 | 41.60 | -0.019 | Bond *et al.* (2006) |
| | Machias Seal Is (2002) | 134 | 33.91 | -0.017 | Bond *et al.* (2006) |
| | Machias Seal Is (2003) | 170 | 26.11 | -0.016 | Bond *et al.* (2006) |
| | Québec (1983) | 145 | 37.28 | -0.018 | Chapdelaine *et al.* (1985) |
| | Rhode Is (1967) | 102 | 35.24 | -0.020 | LeCroy and Collins (1972) |
| | The Netherlands (1989) | 108 | 39.27 | -0.018 | Klaassen *et al.* (1994) |
| | The Netherlands (1990) | 124 | 37.44 | -0.017 | Klaassen (1994) |
| *Sterna paradisaea* | Farne Is, UK (1963) | 73 | 38.42 | -0.021 | Pearson (1968) |
| | Machias Seal Is (1996) | 90 | 44.12 | -0.019 | Bond *et al.* (2006) |
| | Machias Seal Is (1997) | 119 | 40.63 | -0.019 | Bond *et al.* (2006) |
| | Machias Seal Is (1998) | 151 | 27.39 | -0.017 | Bond *et al.* (2006) |
| | Machias Seal Is (2002) | 104 | 40.25 | -0.018 | Bond *et al.* (2006) |
| | Québec (1983) | 125 | 38.74 | -0.018 | Chapdelaine *et al.* (1985) |
| | Svalbard (1986) | 143 | 34.68 | -0.018 | Klaassen *et al.* (1989) |
| | The Netherlands (1989) | 103 | 40.63 | -0.018 | Klaassen *et al.* (1994) |
| | The Netherlands (1990) | 140 | 37.90 | -0.017 | Klaassen (1994) |
| *Sterna sandvicensis* | Farne Is, UK (1963) | 114 | 43.36 | -0.022 | Pearson (1968) |
| | The Netherlands (1998) | 245 | 34.80 | -0.018 | Stienen and Brenninkmeijer (2002) |
| *Sterna sumatrana* | Great Barrier Reef (1986) | 133 | 26.55 | -0.018 | Hulsman and Smith (1988) |
| *Sterna virgata* | Crozet Is (1982) | 94 | 44.17 | -0.017 | Weimerskirch and Stahl (1988) |
| | S Shetland Is (1979) | 166 | 32.50 | -0.017 | Jabłoński (1995) |
| | S Shetland Is (1981) | 216 | 34.48 | -0.016 | Jabłoński (1995) |
| | S Shetland Is (1991) | 159 | 32.91 | -0.018 | Klaassen (1994) |
| **Pelecanidae** | | | | | |
| *Pelecanus occidentalis* | Florida (1972) | 3812 | 20.72 | -0.006 | Schreiber (1976) |
| **Pelecanoididae** | | | | | |
| *Pelecanoides georgicus* | Crozet Is (1982) | 126 | 25.09 | -0.028 | Jouventin *et al.* (1985) |
| *Pelecanoides urinatrix* | Crozet Is (1982) | 134 | 31.40 | -0.015 | Jouventin *et al.* (1985) |

**Appendix 1**. Continued

| Species | Area (Year) | $W_\infty$ | $K$ | $t_o$ | Source |
|---|---|---|---|---|---|
| **Phaethontidae** | | | | | |
| *Phaethon lepturus* | Aldabra Atoll (1968) | 433 | 18.40 | -0.029 | Diamond (1975) |
| | Aldabra Atoll (1969) | 387 | 20.84 | -0.027 | Diamond (1975) |
| | Puerto Rico (1986) | 442 | 25.12 | -0.012 | Schaffner (1990) |
| | Seychelles (2002) | 360 | 21.53 | -0.015 | Ramos and Pacheco (2003) |
| *Phaethon rubricauda* | Aldabra Atoll (1968) | 985 | 15.11 | -0.031 | Diamond (1975) |
| | Aldabra Atoll (1969) | 988 | 11.64 | -0.038 | Diamond (1975) |
| | Christmas Is (1967) | 813 | 23.85 | -0.016 | Schreiber (1994) |
| | Christmas Is (1991) | 624 | 15.80 | -0.030 | Schreiber (1994) |
| | Green Is, Hawaii (1965) | 781 | 22.05 | -0.015 | Fleet (1974) |
| | Johnston Atoll (1986) | 726 | 21.57 | -0.011 | Schreiber (1994) |
| | Johnston Atoll (1991) | 801 | 20.88 | -0.014 | Schreiber (1994) |
| | Johnston Atoll (1992) | 746 | 19.99 | -0.017 | Schreiber (1994) |
| **Phalacrocoracidae** | | | | | |
| *Hypoleucos auritus* | E Bic Reef, Québec (1978) | 1997 | 21.88 | -0.013 | DesGranges (1982) |
| | E Bicquette Is, Québec (1978) | 2446 | 19.09 | -0.009 | DesGranges (1982) |
| | Grand Metis Is, Québec (1978) | 2131 | 21.33 | -0.011 | DesGranges (1982) |
| | Shoals Is, New Hampshire (1972) | 3188 | 19.32 | -0.009 | Dunn (1975) |
| | SW Razade Reef, Québec (1978) | 2288 | 22.07 | -0.011 | DesGranges (1982) |
| | W Bicquette Reef, Québec (1978) | 3462 | 14.45 | -0.007 | DesGranges (1982) |
| *Hypoleucos brasiliensis* | Chile (1997) | 1565 | 12.13 | -0.007 | Kalmbach and Becker (2005) |
| *Microcarbo africanus* | S Africa (1993) | 477 | 33.14 | -0.015 | Kopij (1996) |
| *Microcarbo pygmaeus* | Israel (2001) | 514 | 32.43 | -0.012 | Shmueli *et al*. (2003) |
| *Notocarbo atriceps* | Argentina (1993) | 2475 | 19.58 | -0.012 | Punta *et al*. (2003) |
| | Heard and McDonald Is (1993) | 3312 | 19.93 | -0.012 | Green (1997) |
| | S Georgia (1989) | 2944 | 17.92 | -0.027 | Wanless and Harris (1993) |
| *Phalacrocorax carbo* | Greece (1994) | 2735 | 21.18 | -0.012 | Goutner *et al*. (1997) |
| | Israel (2001) | 2282 | 21.26 | -0.004 | Shmueli *et al*. (2003) |
| *Strictocarbo aristotelis* | Bleiksøy, Norway (1986) | 2712 | 15.85 | -0.011 | Barrett (1989) |
| | Farne Is, UK (1963) | 1027 | 20.60 | -0.013 | Pearson (1968) |
| | Is May, UK (1998) | 1854 | 22.77 | -0.011 | Daunt *et al*. (2001) |
| | Norway (1995) | 2046 | 22.19 | -0.007 | Østnes *et al*. (2001) |
| **Procellariidae** | | | | | |
| *Bulweria bulwerii* | Madeira (1995) | 142 | 34.45 | -0.017 | Nunes and Vicente (1998) |
| *Calonectris diomedea* | Azores (1995) | 1040 | 22.59 | -0.016 | Ramos *et al*. (2003) |
| | Portugal (1987) | 1042 | 25.59 | -0.015 | Granadeiro (1991) |
| | Selvagem Grande (1969) | 895 | 20.83 | -0.026 | Zino (1971) |
| | Selvagem Grande (1991) | 977 | 61.46 | -0.023 | Hamer and Hill (1993) |
| *Daption capense* | S Shetland Is (1992) | 582 | 20.61 | -0.026 | Weidinger (1998) |
| *Fulmarus glacialis* | Shetland Is, UK (1997) | 959 | 29.38 | -0.008 | Phillips and Hamer (2000) |
| | Shetland Is, UK (1997) | 879 | 26.20 | -0.017 | Gray *et al*. (2003) |
| | Shetland Is, UK (1998) | 993 | 25.12 | -0.017 | Gray *et al*. (2003) |

**Appendix 1**. Continued

| **Species** | **Area (Year)** | $W_\infty$ | $K$ | $t_o$ | **Source** |
|---|---|---|---|---|---|
| *Fulmarus glacialoides* | Prydz Bay, Antarctica (1989) | 1059 | 28.59 | -0.018 | Norman and Ward (1992) |
| *Halobaena caerulea* | Crozet Is (1982) | 222 | 28.72 | -0.019 | Jouventin *et al*. (1985) |
| | Prince Edward Is (1983) | 198 | 34.51 | -0.020 | Fugler *et al*. (1987) |
| *Lugensa brevirostris* | Crozet Is (1982) | 308 | 19.76 | -0.052 | Jouventin *et al*. (1985) |
| | Prince Edward Is (1980) | 356 | 29.66 | -0.022 | Schramm (1983) |
| *Macronectes giganteus* | Prince Edward Is (1977) | 4505 | 15.30 | -0.008 | Cooper *et al*. (2001) |
| *Macronectes halli* | Prince Edward Is (1977) | 5194 | 14.43 | -0.011 | Cooper *et al*. (2001) |
| *Pachyptila belcheri* | Falkland Is (1978) | 239 | 29.44 | -0.016 | Strange (1980) |
| | Falkland Is (2003) | 263 | 19.12 | -0.028 | Quillfeldt *et al*. (2007) |
| | Falkland Is (2004) | 181 | 29.15 | -0.018 | Quillfeldt *et al*. (2007) |
| | Falkland Is (2005) | 155 | 31.60 | -0.016 | Quillfeldt *et al*. (2007) |
| *Pachyptila desolata* | S Georgia (1992) | 225 | 35.35 | -0.013 | Reid *et al*. (1999) |
| *Pachyptila salvini* | Crozet Is (1982) | 164 | 19.51 | -0.035 | Jouventin *et al*. (1985) |
| | Prince Edward Is (1981) | 158 | 36.08 | -0.020 | Berruti and Hunter (1986) |
| *Pachyptila turtur* | S Georgia (1983) | 182 | 33.60 | -0.016 | Prince and Copestake (1990) |
| *Pagodroma nivea* | Dronning Maud Land, Antarctica (1985) | 322 | 17.51 | -0.036 | Røv (1990) |
| *Procellaria aequinoctialis* | Prince Edward Is (1981) | 1429 | 20.36 | -0.016 | Berruti *et al*. (1985) |
| | S Georgia (1986) | 1496 | 18.99 | -0.013 | Hall (1987) |
| *Procellaria cinerea* | Kerguelen Is (1988) | 1394 | 13.14 | -0.038 | Zotier (1990a) |
| | Prince Edward Is (1982) | 1247 | 17.31 | -0.015 | Newton and Fugler (1989) |
| *Pseudobulweria rostrata* | New Caledonia (2004) | 583 | 15.52 | -0.047 | Villard *et al*. (2006) |
| *Pterodroma arminjoniana* | Mauritius (1978) | 513 | 22.83 | -0.024 | Gardner *et al*. (1985) |
| *Pterodroma atrata* | Pitcairn Is (1990) | 379 | 25.86 | -0.015 | de L. Brooke (1995) |
| *Pterodroma axillaris* | Chatham Is, New Zealand (1997) | 328 | 26.44 | -0.013 | Gardner (1999) |
| *Pterodroma hypoleuca* | Midway Atoll, Hawaii (1981) | 239 | 24.75 | -0.022 | Pettit *et al*. (1982) |
| *Pterodroma incerta* | Gough Is (2001) | 762 | 5.89 | -0.118 | Cuthbert (2004) |
| *Pterodroma lessoni* | Kerguelen Is (1987) | 108 | 16.13 | -0.023 | Zotier (1990b) |
| *Pterodroma leucoptera* | New South Wales, Australia (2001) | 279 | 17.07 | -0.038 | O'Dwyer *et al*. (2006) |
| *Pterodroma macroptera* | Prince Edward Is (1980) | 444 | 20.41 | -0.022 | Schramm (1983) |
| | Prince Edward Is (1982) | 621 | 12.84 | -0.037 | Newton and Fugler (1989) |
| *Pterodroma mollis* | Crozet Is (1982) | 295 | 18.60 | -0.038 | Jouventin *et al*. (1985) |
| | Prince Edward Is (1980) | 341 | 22.44 | -0.024 | Schramm (1983) |
| *Pterodroma nigripennis* | Lord Howe Is, Australia (1990) | 237 | 21.31 | -0.024 | Hutton and Priddel (2002) |
| *Pterodroma phaeopygia* | Galápagos (1986) | 536 | 18.03 | -0.032 | Cruz and Cruz (1990) |
| | Galápagos (1966) | 423 | 22.04 | -0.034 | Harris (1970b) |
| | Hawaii (1981) | 540 | 19.84 | -0.018 | Simons (1985) |
| *Pterodroma pycrofti* | New Zealand (2001) | 227 | 50.45 | -0.025 | Gangloff and Wilson (2004) |
| *Puffinus assimilis* | Lord Howe Is, Australia (1989) | 222 | 28.83 | -0.014 | Priddel et al. (2003) |
| | New Zealand (1994) | 278 | 24.13 | -0.016 | Booth et al. (2000) |
| *Puffinus gravis* | Gough Is (2001) | 1157 | 21.12 | -0.020 | Cuthbert (2005) |
| *Puffinus griseus* | New Zealand (1944) | 1147 | 11.50 | -0.035 | Richdale (1945) |
| *Puffinus huttoni* | New Zealand (1999) | 507 | 23.17 | -0.023 | Cuthbert and Davis (2002) |
| *Puffinus opisthomelas* | Natividad Is, Mexico (1998) | 395 | 25.96 | -0.019 | Keitt et al. (2003) |

**Appendix 1**. Continued

| **Species** | **Area (Year)** | $W_\infty$ | $K$ | $t_o$ | **Source** |
|---|---|---|---|---|---|
| *Puffinus pacificus* | Kilauea Point, Hawaii (1978) | 489 | 14.00 | -0.039 | Pettit et al. (1984b) |
| | Kilauea Point, Hawaii (1979) | 479 | 21.89 | -0.025 | Pettit et al. (1984b) |
| | Kilauea Point, Hawaii (1980) | 456 | 18.10 | -0.031 | Pettit et al. (1984b) |
| | Manana Is, Hawaii (1978) | 427 | 19.19 | -0.029 | Pettit et al. (1984b) |
| | Manana Is, Hawaii (1979) | 441 | 18.88 | -0.030 | Pettit et al. (1984b) |
| | Manana Is, Hawaii (1984) | 476 | 14.50 | -0.044 | Fry et al. (1986) |
| | Tern Is, Hawaii (1979) | 503 | 15.86 | -0.033 | Pettit et al. (1984b) |
| *Puffinus puffinus* | Faeroe Is (1981) | 427 | 28.02 | -0.015 | Bech et al. (1982) |
| | Wales, UK (1995) | 559 | 23.71 | -0.016 | Hamer and Hill (1997) |
| | Wales, UK (1996) | 525 | 22.96 | -0.018 | Hamer et al. (1998) |
| | Wales, UK (1999) | 680 | 20.55 | -0.010 | Gray et al. (2005) |
| *Puffinus tenuirostris* | Great Dog Is, Australia (1995) | 930 | 12.85 | -0.032 | Hamer et al. (1997) |
| *Thalassoica antarctica* | Dronning Maud Land, Antarctica (1984) | 640 | 23.89 | -0.022 | Røv (1990) |
| | Dronning Maud Land, Antarctica (1985) | 1058 | 15.57 | -0.027 | Haftorn et al. (1991) |
| | Dronning Maud Land, Antarctica (1992) | 852 | 22.14 | -0.023 | Lorentsen (1996) |
| | Prydz Bay, Antarctica (1989) | 1057 | 30.53 | -0.017 | Norman and Ward (1992) |
| **Spheniscidae** | | | | | |
| *Aptenodytes patagonicus* | Crozet Is (2000) | 5797 | 12.22 | -0.024 | de Margerie et al. (2004) |
| | Heard and McDonald Is (1992) | 11010 | 9.38 | -0.007 | Moore *et al.* (1998) |
| | Prince Edward Is (1989) | 10033 | 7.56 | -0.037 | van Heezik *et al.* (1993) |
| *Eudyptes chrysocome* | Macquarie Is (1956) | 2786 | 17.35 | -0.010 | Warham (1963) |
| | Macquarie Is (1994) | 2763 | 14.87 | -0.004 | Hull *et al.* (2004) |
| | Macquarie Is (1995) | 2551 | 11.67 | -0.013 | Hull *et al.* (2004) |
| | Macquarie Is (1996) | 2808 | 14.96 | -0.010 | Hull *et al.* (2004) |
| | Prince Edward Is (1985) | 1902 | 20.26 | -0.015 | Brown (1987) |
| *Eudyptes chrysolophus* | Prince Edward Is (1985) | 2609 | 15.57 | -0.035 | Brown (1987) |
| | S Georgia (1986) | 4739 | 14.56 | -0.017 | Williams (1990) |
| | S Georgia (1998) | 4369 | 11.89 | -0.030 | Barlow and Croxall (2002) |
| | S Georgia (1999) | 3502 | 18.00 | -0.015 | Barlow and Croxall (2002) |
| | S Georgia (2000) | 4302 | 14.00 | -0.026 | Barlow and Croxall (2002) |
| *Eudyptula minor* | Penguin Is, Australia (1989) | 1018 | 25.46 | -0.016 | Wienecke *et al.* (2000) |
| | Penguin Is, Australia (1990) | 1190 | 23.54 | -0.017 | Wienecke *et al.* (2000) |
| | Penguin Is, Australia (1991) | 1242 | 21.77 | -0.016 | Wienecke *et al.* (2000) |
| *Megadyptes antipodes* | New Zealand (1937) | 6026 | 13.37 | -0.004 | van Heezik (1991) |
| | New Zealand (1938) | 7563 | 9.74 | -0.020 | van Heezik (1991) |
| | New Zealand (1940) | 5640 | 13.10 | -0.012 | van Heezik (1991) |
| | New Zealand (1984) | 6543 | 14.11 | -0.003 | van Heezik (1990) |
| | New Zealand (1985) | 6078 | 13.76 | -0.013 | van Heezik (1990) |
| | New Zealand (1986) | 4184 | 17.69 | -0.010 | van Heezik (1990) |

**Appendix 1**. Continued

| Species | Area (Year) | $W_\infty$ | $K$ | $t_o$ | Source |
|---|---|---|---|---|---|
| *Pygoscelis adeliae* | Humble Is, Antarctica (1989) | 4134 | 17.47 | -0.016 | Salihoglu *et al.* (2001) |
| | Humble Is, Antarctica (1990) | 5749 | 8.67 | -0.072 | Salihoglu *et al.* (2001) |
| | Lützow-Holm Bay, Antarctica (1989) | 5107 | 16.52 | -0.032 | Watanuki *et al.* (1992) |
| | Lützow-Holm Bay, Antarctica (1990) | 3983 | 20.84 | -0.021 | Watanuki *et al.* (1992) |
| | Lützow-Holm Bay, Antarctica (1991) | 2567 | 32.00 | -0.020 | Watanuki *et al.* (1992) |
| | Ross Is, Antarctica (1970) | 3420 | 22.97 | -0.015 | Ainley and Schlatter (1972) |
| | Torgersen Is, Antarctica (1989) | 3651 | 16.77 | -0.042 | Salihoglu *et al.* (2001) |
| | Torgersen Is, Antarctica (1990) | 5190 | 9.57 | -0.064 | Salihoglu *et al.* (2001) |
| *Pygoscelis antarctica* | S Shetland Is (1980) | 3914 | 22.55 | -0.012 | Taylor (1985) |
| | S Shetland Is (1990) | 4058 | 22.33 | -0.020 | Croll *et al.* (2006) |
| | S Shetland Is (1991) | 4643 | 17.05 | -0.014 | Croll *et al.* (2006) |
| | S Shetland Is (1992) | 4621 | 19.06 | -0.015 | Croll *et al.* (2006) |
| | S Shetland Is (1993) | 3170 | 21.54 | -0.013 | Moreno *et al.* (1994) |
| *Pygoscelis papua* | S Shetland Is (1980) | 6739 | 13.55 | -0.012 | Taylor (1985) |
| *Spheniscus demersus* | S Africa (1974) | 1930 | 14.62 | -0.026 | Cooper (1977) |
| *Spheniscus magellanicus* | Argentina (1991) | 3840 | 12.63 | -0.018 | Frere *et al.* (1998) |
| | Argentina (1992) | 5030 | 9.53 | -0.028 | Frere *et al.* (1998) |
| | S Chile (1997) | 3667 | 18.18 | -0.008 | Radl and Culik (1999) |
| **Stercorariidae** | | | | | |
| *Catharacta antarctica* | S Georgia (2001) | 2199 | 16.89 | -0.013 | Phillips *et al.* (2004) |
| | S Georgia (2002) | 1808 | 20.53 | -0.012 | Phillips *et al.* (2004) |
| | S Georgia (2003) | 1938 | 20.55 | -0.011 | Phillips *et al.* (2004) |
| *Catharacta maccormicki* | Prydz Bay, Antarctica (1990) | 1726 | 14.86 | -0.030 | Wang and Norman (1993) |
| | S Shetland Is (2001) | 1347 | 23.05 | -0.012 | Ritz *et al.* (2005) |
| *Stercorarius longicaudus* | E Greenland (1975) | 306 | 31.88 | -0.015 | de Korte (1986) |
| **Sulidae** | | | | | |
| *Morus bassanus* | Baccalieu Is, Newfoundland (1979) | 4123 | 17.54 | -0.006 | Montevecchi *et al.* (1984) |
| | Magdalen Is, Québec (1979) | 4477 | 15.48 | -0.011 | Kirkham and Montevecchi (1982) |
| | Québec (1965) | 4708 | 15.15 | -0.011 | Poulin (1968) |
| | Scotland, UK (1962) | 4746 | 15.39 | -0.008 | Nelson (1964) |
| | Scotland, UK (1976) | 4732 | 15.33 | -0.008 | Wanless (1984) |
| *Morus capensis* | S Africa (1967) | 3390 | 15.81 | -0.009 | Jarvis (1974) |
| | S Africa (1974) | 3671 | 14.81 | -0.007 | Cooper (1978) |
| | S Africa (1988) | 3461 | 15.41 | -0.009 | Navarro (1991) |
| *Morus serrator* | Victoria, Australia (1995) | 3668 | 15.82 | -0.006 | Gibbs *et al.* (2000) |
| | Victoria, Australia (1999) | 3457 | 16.58 | -0.007 | Bunce (2001) |
| *Sula dactylatra* | Ascension Is (1960) | 1952 | 17.60 | -0.009 | Dorward (1962) |
| | Kure Atoll, Hawaii (1965) | 2107 | 18.25 | -0.001 | Kepler (1969) |
| | Lord Howe Is, Australia (2002) | 2260 | 17.74 | -0.011 | Priddel *et al.* (2005) |
| *Sula nebouxii* | Galápagos (1964) | 1939 | 14.74 | -0.005 | Duffy and Ricklefs (1981) |
| | Lobos de Tierra Is, Peru (1979) | 1669 | 19.54 | -0.020 | Duffy and Ricklefs (1981) |
| *Sula sula* | Galápagos (1963) | 956 | 9.63 | -0.014 | Nelson (1969) |

# GROWTH OF MARINE REPTILES[1]

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## ABSTRACT

Growth data were obtained from the scientific literature and re-expressed according to the von Bertalanffy Growth Function (VBGF) using a variety of methods. This resulted in 103 population estimates of VBGF parameters for 27 species of marine reptiles, i.e., marine iguana, saltwater crocodile, 8 species of sea turtles and 16 species of aquatic snakes. A frequency distribution of the growth performance index ($\Phi'$) values indicate two peaks, i.e., index values at 2.75 for sea turtles and marine iguana and at 3.75 for sea snakes, while saltwater crocodiles have index values at the tail of the distribution (4.75-5.25). The auximetric plot of $log_{10}K$ against $log_{10}W_\infty$ indicates that like marine mammals, seabirds and invertebrates, marine reptiles exhibit the same growth patterns as those of fish and thus, their growth can be expressed according to the VBGF.

## INTRODUCTION

Marine reptiles consist of 77 species belonging to 4 major groups, i.e., marine iguana (1 species), saltwater crocodile (1), sea turtles (8) and sea snakes (67; Kharin, 2008, see Bell, 1843). Sea turtles are circumglobal whereas sea snakes are distributed mostly around the eastern Indo-Pacific region. The marine iguana, *Crocodylus porosus*, is endemic to the Galapagos Islands (Kruuk & Snell, 1981). The crocodile, *Amblyrhynchus cristatus*, is the only crocodile inhabiting marine and freshwaters in the Indo-Pacific (Mead *et al.*, 2002). There are 9 reptile species included in the IUCN Red List of Threatened Species (2007), which include 7 species of sea turtles, i.e., 3 are listed as critically endangered (*Dermochelys coriacea*, *Eretmochelys imbricata*, *Lepidochelys kempii*), 3 as endangered (*Caretta caretta*, *Chelonia mydas*, *Lepidochelys olivacea*) and *Natator depressus* as data defficient, the marine iguana, *Amblyrhynchus cristatus* is listed as vulnerable, and the Atlantic salt marsh snake, *Nerodia clarkii* as of least concern (see also Ineich & Laboute 2002). These 9 species represent 12% of all species of marine reptiles existing in the world, which is a high percentage; it is due to the fact that these animals grow to large sizes and have slower metabolic and turn over rates.

In spite of reptiles' vulnerability to extinction, studies on reptilian life history are few and usually serological in nature (e.g., Rogers, 1902-1903) and are usually on terrestrial species, e.g., on sexual dimorphism and diet (e.g., Shine *et al.*, 2002; Camilleri & Shine, 1990), reproductive strategies (e.g., Shine, 1988; Lemen & Voris, 1981), body size (e.g., Boback & Guyer, 2003) and patterns of growth (e.g., Shine & Charnov, 1992). Most studies focusing on sea snakes lack discussions on the growth of these

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animals and even the review of sea snake biology by Dunson (1975), though comprehensive, did not include growth.

Recent interest, notably on the effect of trawl fisheries to sea snake populations, e.g., in Australia (Ward, 2001; Fry *et al.*, 2001; Ward, 2000) indicate a need for growth parameters for sea snakes. In response to this, growth data were compiled from various published references. In addition, these were used to confirm that the von Bertalanffy Growth Function (VBGF) can indeed describe the growth of marine reptiles as suggested for snakes and lizards in Shine & Charnov (1992) and for sea turtles in Jones *et al.* (2008) even though they have body shapes, i.e., elongate or box-like, different from fish, for which the VBGF has been largely used.

The data assembled here and the VBGF parameters estimated will be made available via the online information system, SeaLifeBase (www.sealifebase.org) in the hope that they could be used in the assessment and management of marine reptilian stocks.

## MATERIAL AND METHODS

### *Growth parameter estimation*

Growth data for species in their natural environment (wild) representing a reasonable range of sizes were assembled from various published literature, i.e., (i) growth parameter estimates; (ii) length-at age or growth increment data; and (iii) length-frequency distributions (carapace length (CL) for sea turtles and snout-vent length (SVL) for sea snakes, marine crocodile and iguana). Data in (i), if expressed in functions other than the von Bertalanffy Growth Function (VBGF), e.g., Gompetz and logistic curves, were re-expressed as VBGF parameters. Data in (ii) were fitted directly to the von Bertalanffy growth function (von Bertalanffy, 1957):

$$L_t = L_\infty(1\text{-}e^{-K(t-t0)}) \qquad \ldots\ 1)$$

where $L_t$ is the length at age $t$, $L_\infty$ is the asymptotic length, $K$ is a growth coefficient (growth rate towards the maximum), and $t_o$ is the age at which length is zero.

Data in (iii) were fitted to the Powell-Wetherall Plot (PW-Plot; see Pauly, 1998; Wetherall, 1986; Powell, 1979) to estimate $L_\infty$, based on the assumption that the resulting distribution is representative of the population. The PW-Plot consists of pointer parameters, i.e., mean ($L_{mean}$) and cut off ($L_i$) lengths. A series of mean lengths ($L_{mean}$), computed from successive cut-off lengths ($L_{i+1}$), minus the $L_i$ (i.e., $L_{mean}$-$L_i$) are plotted against $L_i$. The resulting downward trend of points were fitted to a linear regression where $L_\infty$ is estimated as $a/-b$ and $Z/K$ as $(1+b)/(-b)$, $Z$ being the total instantaneous mortality of an exploited population, and conversely, is equivalent to $M$ (natural mortality) if the population being studied is not exploited (see below). In cases where the data in (iii) were comprised of successive length-frequency distributions, the data were fitted to the VBGF using a non-parametric, robust approach known as ELEFAN (Pauly, 1987; 1998), implemented in the FiSAT software package (Gayanilo *et al.*, 1996).

In cases where only $L_\infty$ estimates were available, e.g., results of the PW-Plot, values of K were obtained using the growth performance index ($\Phi'$) defined by Pauly & Munro (1984) as $\Phi' = log_{10} K + 2{\cdot}log_{10}L_\infty$, and mean values of $\Phi'$, available from $L_\infty$ and $K$ pairs for: (a) the same species in different localities; (b) other species in the same genus; (c) other species in the same family. Estimates of $K$ obtained in this fashion are marked as such in SeaLifeBase and thus can be ignored when only independent estimates are sought.

### *Asymptotic weight estimation*

Asymptotic weight, $W_\infty$, was estimated using the length-weight relationship of the form

$$W = a \cdot L^b \qquad \ldots\ (2)$$

where $a$ is a multiplicative term equivalent to the y-intercept of the log-log transformed linear regression, $L$ the asymptotic length, and $b$ the isometric weight growth parameter, equivalent to the slope of the regression. In cases where sufficient length-weight data pairs were not available for linear regression analyses, condition factors (*c.f.*) using individual length-weight pairs were estimated with

$c.f. = W \cdot 100/L^3$, where $W$ is the weight in grams, and $L$ the length in centimeters (Pauly, 1984b). The value of the length-weight parameter $a$ was then obtained as $a = c.f./100$, assuming that $b$=3. All lengths are expressed in centimeters and weights in grams.

*Mortality estimation*

The total instantaneous mortality (Z) of a given population is defined as:

$$N_{t_2} = N_{t_1} \cdot e^{-Z \cdot (t_2 - t_1)} \qquad \text{... 3)}$$

where $N_{t_1}$ and $N_{t_2}$ is the population size at time $t_1$ and $t_2$, respectively (Koch *et al.*, 2007). The parameter $Z$ is the sum of natural mortality ($M$) and fishing mortality ($F$). As marine reptiles are exploited, either by a target fishery or as by-catch, we can assume that the mortalities inferred from equation (3) refer to total mortality. The data in (iii), as discussed above, were plotted with the Powell-Wetherall Plot to infer $Z/K$ assuming that the samples are representative of the population in the juvenile and adult phases (Wetherall, 1986; Wetherall *et al.*, 1987). Where applicable, length-frequency samples were converted to catch curves, using the growth parameters obtained from FiSAT ((Pauly, 1987; 1998; Gayanilo *et al.*, 1996) to obtain estimates of total mortality. All mortalities are expressed in years$^{-1}$.

## RESULTS AND DISCUSSION

Growth data were found for 92 populations of 26 marine reptile species. Sea turtles represent half of this available data, perhaps due to the fact that they are endangered and thus the need to study and understand their biology instigates baseline studies. Sea snakes, the other group which is well-represented in this study, are an important by-catch in Australian trawl fisheries protected under Schedule 1 of the National Parks and Wildlife Regulations since 1994 (Milton, 2005; 2001) and are thus the subject of research programs in Australia. Here, survey data, graciously provided by the Australian Fisheries Research and Development Corporation and Commonwealth Scientific and Industrial Research Organisation in collaboration with fishers from the Australian Northern Prawn Fishery were used to obtain length-frequency distributions analyzed with ELEFAN to estimate $L_\infty$ for 13 species of sea snakes from the Gulf of Carpentaria.

**Table 1.** Summary of marine reptile growth data obtained from the scientific literature. Details of growth data are included in Table A1.

| Order | Family | No. spp | No. stocks | $L_\infty$ $K$ | $L_\infty$ $Z/K$ | $L/W$ | $c.f.$ | $Z$ | $L_m$ |
|---|---|---|---|---|---|---|---|---|---|
| Crocodilia | Crocodylidae | 1 | 3 | 2 | - | 1 | - | 1 | - |
| Squamata | Acrochordidae | 1 | 2 | 2 | 2 | - | 2 | - | - |
| | Colubridae | 1 | 2 | 2 | - | 1 | - | 2 | - |
| | Hydrophiidae | 15 | 20 | 10 | 21 | 36 | 102 | 4 | 53 |
| | Iguanidae | 1 | 4 | 1 | 2 | - | 5 | 1 | - |
| Testudines | Cheloniidae | 7 | 58 | 26 | 31 | 11 | 4 | 4 | 2 |
| | Dermochelyidae | 1 | 3 | 1 | 3 | 3 | 5 | - | - |
| Total | - | 27 | 92 | 43 | 69 | 52 | 103 | 12 | 55 |

The results of this study, summarized in Table 1, show that life history data on marine reptiles do exist, though not standardized in a format that could be readily used for management purposes. The standardization performed here included the following: (i) converting length units in centimeters (cm), weight units in grams (g) and age units in years; (ii) expressing lengths in the same length type, i.e., snout-vent length for most marine reptiles and carapace length for sea turtles; (iii) re-expressing growth through the VBGF; and (iv) converting L/W relationships to cm and g. All conversions were straighforward except for item (ii), notably for sea turtles where curved and straight carapace lengths (CCL and SCL, respectively) are used. Empirical equations based on simple linear regression of paired SCL and CCL data were adapted from Teas (1993; p. 3) and used to convert values of $CCL_\infty$ to $SCL_\infty$ (see details in Table A1) and *vice versa* depending on the length type used in the length-weight relationships.

The frequency histogram of the L/W relationship coefficient $b$ values obtained for 52 populations using linear regressions of length and weight data pairs (Figure 1) shows a clear peak at size class b=3 (median value is 2.96 and the mode is at 3.00; s.d.=0.36; sample variance of 0.13). This suggests that marine reptiles grow like marine mammals (see Palomares *et al.*, 2008), seabirds (see Karpouzi & Pauly, 2008) and fish (see Carlander, 1969; 1977).

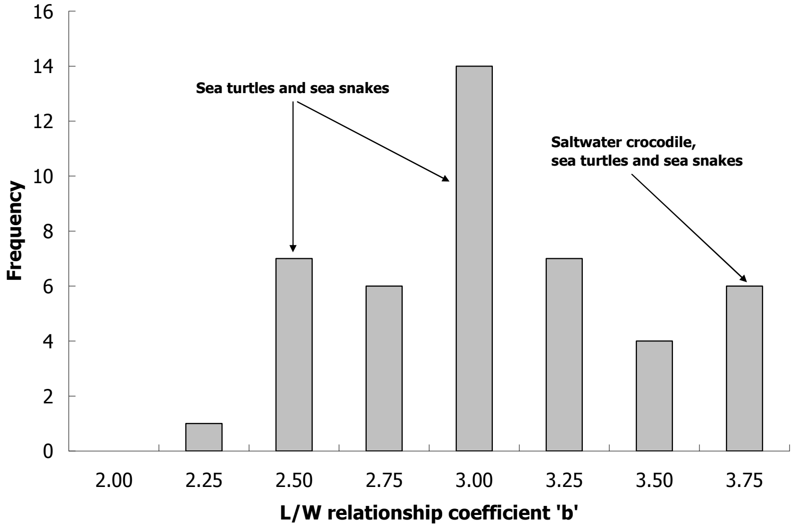

**Figure 1.** Distribution of length-weight relationship coefficient b of 53 populations of marine reptiles (see TableA1 for details).

The asymptotic lengths obtained ranged from 28.6 cm (*Amblyrhynchus cristatus*, Galapagos Islands) to 323 cm (*Crocodylus porosus*, Northern Territory, Australia). Sea snakes ranged in size from 66.8 cm (*Emydocephalus ijimae*, Zamamijima, Ryukyu Island) to 257 cm (*Hydrophis elegans*, Gulf of Carpentaria, Australia) while sea turtles ranged in size from 56.2 cm (*Lepidochelys kempii*, Sambine Pass, Gulf of Meixco, USA) to 168 cm (*Chelonia mydas*, Great Inagua, Bahamas). The auximetric grid plotting *log K* against *log* $W_\infty$ (Figure 2) indicates that marine iguanas grow similarly to sea snakes, while saltwater crocodiles, though clearly a group apart, grow more similarly to sea turtles. Note however, three outliers, i.e., *Chelonia mydas* (Table A2, 21g), *Lepidochelys kempii* (see Table A2, 24a) and *Dermochelys coriacea* (Table A2, 27d). Though the sample size range (26-72 cm) of the *C. mydas* population is wide enough to include juveniles and adults, this range probably represent sub-adult populations given that the largest length in the sample is only 70% of $L_{max}$ ($L_{max}$ = 105 cm CL; Schneider, 1990) and only 43% of the largest $L_\infty$ reported for this species (i.e., 168 cm SCL; see Table A2, 21k). The same could be argued for the *L. kempii* population (sample length range=20-60 cm) which grow to Lmax=75 cm CL (Carr and Caldwell, 1956). However, note that the growth parameters for this population were obtained from a single length-frequency histogram using the Powell-Wetherall Plot and K from *Φ'*. The last sea turtle outlier, *D. coriacea* came from measurements of turtles sampled from tropical areas (see Jones *et al.*, 2008) and reared in captivity in Vancouver, Canada to more than 2 years of age, i.e., to only 60% of the recorded $L_{max}$ (257 cm CL; Márquez, 1990). The growth parameters of the outlier sea snake population of *Astrotia stokesii* were obtained from survey samples of the AFRDC, CSIRO and NPF (Australia) and the Powell-Wetherall Plot. Though the $L_\infty$ estimate may be viable, the K estimate, obtained from the average *Φ'* for species in the family

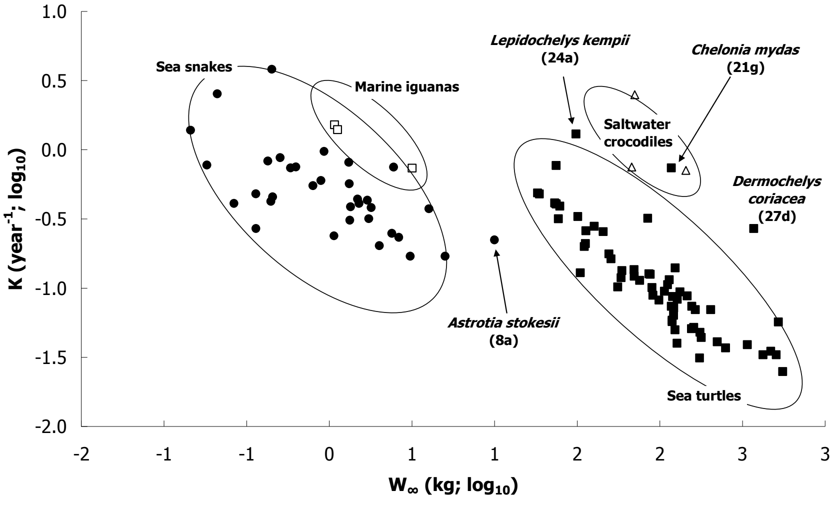

**Figure 2.** Auximetric plot of von Bertalanffy growth parameters for 92 populations of 26 species of marine reptiles (see Table A2 for details). Note similarity of growth performance of sea snakes with marine iguanas and saltwater crocodiles with sea turtles. The 3 outlier populations of sea turtles are based on length-frequency samples with narrow length ranges, i.e., juveniles, while the outlier snake population's K was estimated from the average Φ' of species in the family Hydrophiidae.

Hydrophiidae and is not an independent estimate.

Average values of Z/K for sea snakes and sea turtles are 2.07 (s.e. = 0.231) and 1.4 (s.e. = 0.115), respectively (see Figure 3). These values are comparable with those reported for fishes, i.e., 1.00-2.00 (Beverton and Holt 1956, Pauly 1998). The Z/K values available for marine iguanas are 1.24 and 1.76, also within the range given for fishes. Values of natural mortality for 12 species of marine reptiles ranged from 0.16 (*Chelonia mydas*, Bahia Magdalena, Mexico) to 4.83 (*Amblyrhynchus cristatus*, Genovesa, Galapagos Island).

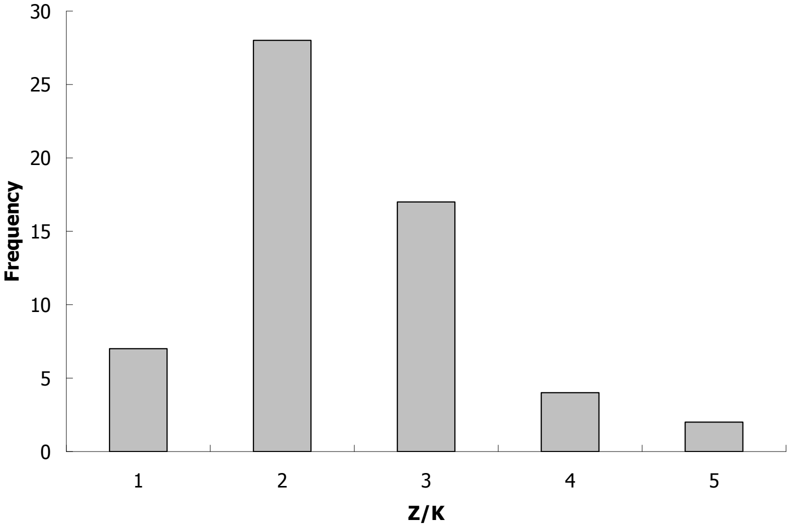

**Figure 3.** Frequency distribution of Z/K values obtained for sea snakes and sea turtles with average values of 2.07 (s.e. = 0.231) and 1.4 (s.e. = 0.115), respectively (see Table A2 for details).

Length at maturity assembled for sea snakes ranged from 42.5 cm (*Thalassophis anomalus*, Sourabaya, Java, Indonesia) to 145 cm (*Disteira kingii*, northern Australia). This data set was used with the available growth parameter estimates for the same population to obtain a frequency histogram of the reproductive load for sea snakes, i.e., $L_m/L_\infty$ values (Figure 4), which ranged from 0.400 (*Astrotia stokesii*, northern Australia) to 0.832 (*Disteira kingii*, northern Australia), with a mean value of 0.582 (s.e. = 0.0221). Only two populations of sea turtles, i.e., *Lepidochelys kempii*, have available $L_m$ data and for which reproductive load were calculated (see Figure 4). Figure 4 emulates the negative trend found for fish (Pauly 1984a) and reiterates the result that marine reptiles grow like fish.

This study is the first to compile data on growth of marine reptiles. Only 16 percent of the total species stated in the introduction were covered in this study. However, more work is necessary in order to further understand the biology of marine reptiles and help prevent marine reptile species, e.g., sea turtles, from being farther endangered.

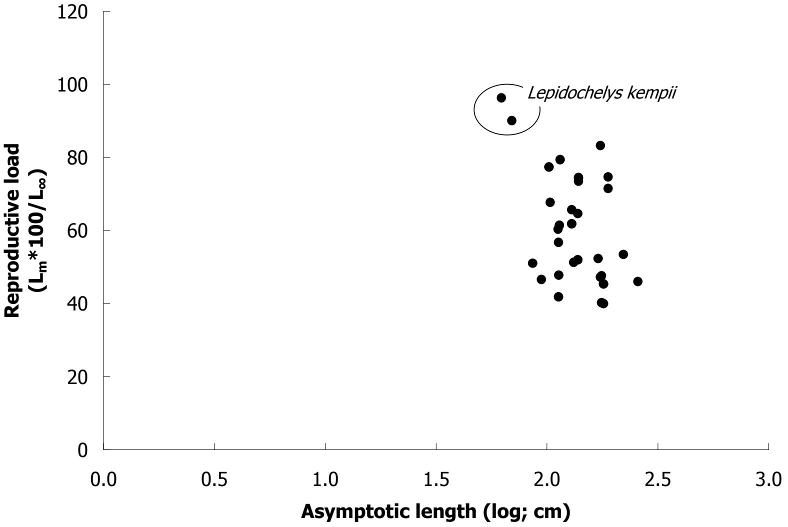

**Figure 4.** Reproductive load plotted against asymptotic length of 35 populations of sea snakes (12 species) and 2 populations of sea turtles, *Lepidochelys kempii*. Note negative trend emulating what has been found for fish (see details in Table A3).

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**Table A1**. Length-weight data for marine reptiles used to obtain Figure 1. TL=total length; SVL=snout-vent length; SCL=straight carapace length; CCL=curved carapace length; CL=carapace length.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | $r^2$ | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | a | *Crocodylus porosus* (Crocodilla, Crocrodylidae) | Cape York Peninsula, Australia | 11 | M | TL | 3.60 | 0.0001 | - | 0.998 | Grigg *et al.* (1998; Tab. 1 p. 1793). |
| 2 | a | *Acrochordus granulatus* (Squamata, Acrochordidae) | Phangnga Bay, Thailand | 45 | F | SVL | 3.00 | 0.0005 | 0.0521 | - | a from c.f. of data from Wangkulangkul *et al.* (2005; Fig. 2, p. 259). |
|  | b |  | Phangnga Bay, Thailand | 19 | M | SVL | 3.00 | 0.0004 | 0.0384 | - | a from c.f. of data from Wangkulangkul *et al.* (2005; Fig. 2, p. 259). |
| 3 | a | *Cerberus rynchops* (Squamata, Colubridae) | Muar River, Malaysia | 14 | unsexed | SVL | 3.01 | 0.0006 | - | 0.992 | Jayne *et al.* (1988; Tab. 5, p. 10). Results maybe biased because N is small. |
| 4 | a | *Acalyptophis peronii* (Squamata, Hydrophiidae) | East coast, northern Australia | - | unsexed | SVL | 3.00 | 0.0011 | 0.1095 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
|  | b |  | Groote, northern Australia | 1 | M | SVL | 3.00 | 0.0008 | 0.0797 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
|  | c |  | Gulf of Carpentaria, Australia | 22 | F | SVL | 3.29 | 0.0002 | - | 0.974 | Survey data from AFRDC, CSIRO, NPF. |
|  | d |  | Gulf of Carpentaria, Australia | 24 | M | SVL | 2.70 | 0.0028 | - | 0.937 | Survey data from AFRDC, CSIRO, NPF. |
|  | e |  | Gulf of Carpentaria, Australia | 50 | unsexed | SVL | 3.00 | 0.0007 | - | 0.851 | Survey data from AFRDC, CSIRO, NPF. |
|  | f |  | Mornington, northern Australia | - | mixed | SVL | 3.00 | 0.0007 | 0.0670 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
|  | g |  | Weipa, northern Australia | 9 | mixed | SVL | 3.00 | 0.0008 | 0.0765 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 5 | a | *Aipysurus apraefrontalis* | northwestern Shelf, Australia | 1 | M | SVL | 3.00 | 0.0007 | 0.0700 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 6 | a | *Aipysurus duboisii* | East coast, northern Australia | - | M | SVL | 3.00 | 0.0008 | 0.0814 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
|  | b |  | Groote, northern Australia | 3 | F | SVL | 3.00 | 0.0006 | 0.0612 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
|  | c |  | Gulf of Carpentaria, Australia | 8 | F | SVL | 3.00 | 0.0006 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. |
|  | d |  | Gulf of Carpentaria, Australia | 11 | M | SVL | 3.00 | 0.0005 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. |
|  | e |  | Gulf of Carpentaria, Australia | 20 | unsexed | SVL | 2.90 | 0.0009 | - | 0.720 | Survey data from AFRDC, CSIRO, NPF. |
|  | f |  | Mornington, northern Australia | 2 | M | SVL | 3.00 | 0.0006 | 0.0583 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
|  | g |  | Weipa, northern Australia | 3 | mixed | SVL | 3.00 | 0.0005 | 0.0486 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |

**Table A1**. Continued.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | $r^2$ | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 7 | a | *Aipysurus eydouxii* | East coast, northern Australia | - | F | SVL | 3.00 | 0.0012 | 0.1156 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | b | | Groote, northern Australia | 12 | mixed | SVL | 3.00 | 0.0012 | 0.1236 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | c | | Gulf of Carpentaria, Australia | 75 | F | SVL | 2.48 | 0.0099 | - | 0.843 | Survey data from AFRDC, CSIRO, NPF. |
| | | | Gulf of Carpentaria, Australia | 28 | F | SVL | 3.00 | 0.0008 | 0.0845 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | e | | Gulf of Carpentaria, Australia | 24 | M | SVL | 2.50 | 0.0096 | - | 0.786 | Survey data from AFRDC, CSIRO, NPF. |
| | f | | Gulf of Carpentaria, Australia | 30 | M | SVL | 3.00 | 0.0010 | 0.0973 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | g | | Gulf of Carpentaria, Australia | 104 | unsexed | SVL | 2.60 | 0.0061 | - | 0.866 | Survey data from AFRDC, CSIRO, NPF. |
| | h | | Mornington, northern Australia | - | mixed | SVL | 3.00 | 0.0014 | 0.1364 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | i | | Weipa, northern Australia | 18 | F | SVL | 3.00 | 0.0012 | 0.1233 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 8 | a | *Aipysurus laevis* | East coast, northern Australia | - | unsexed | SVL | 3.00 | 0.0010 | 0.1008 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | b | | Groote, northern Australia | 7 | mixed | SVL | 3.00 | 0.0015 | 0.1485 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | c | | Gulf of Carpentaria, Australia | 36 | F | SVL | 3.62 | 0.0001 | - | 0.954 | Survey data from AFRDC, CSIRO, NPF. |
| | d | | Gulf of Carpentaria, Australia | 19 | F | SVL | 3.00 | 0.0013 | 0.1281 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | e | | Gulf of Carpentaria, Australia | 36 | M | SVL | 3.00 | 0.0011 | - | 0.881 | Survey data from AFRDC, CSIRO, NPF. |
| | f | | Gulf of Carpentaria, Australia | 12 | M | SVL | 3.00 | 0.0012 | 0.1233 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| 8 | g | *Aipysurus laevis* | Gulf of Carpentaria, Australia | 74 | unsexed | SVL | 3.52 | 0.0001 | - | 0.900 | Survey data from AFRDC, CSIRO, NPF. |
| | h | | Mornington, northern Australia | 2 | F | SVL | 3.00 | 0.0013 | 0.1316 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | i | | Torres Strait, Australia | 1 | M | SVL | 3.00 | 0.0011 | 0.1136 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | j | | Weipa, northern Australia | 14 | mixed | SVL | 3.00 | 0.0012 | 0.1188 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 9 | a | *Astrotia stokesii* | Darwin, northern Australia | 1 | M | SVL | 3.00 | 0.0012 | 0.1231 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | b | | East coast, northern Australia | - | unsexed | SVL | 3.00 | 0.0011 | 0.1081 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |

**Table A1**. Continued.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | $r^2$ | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 9 | c | *Astrotia stokesii* | Gulf of Carpentaria, Australia | 71 | F | SVL | 3.58 | 0.0001 | - | 0.895 | Survey data from AFRDC, CSIRO, NPF. |
| | d | | Gulf of Carpentaria, Australia | 16 | F | SVL | 3.00 | 0.0015 | 0.1547 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | e | | Gulf of Carpentaria, Australia | 57 | M | SVL | 3.07 | 0.0008 | - | 0.856 | Survey data from AFRDC, CSIRO, NPF. |
| | f | | Gulf of Carpentaria, Australia | 10 | M | SVL | 3.00 | 0.0010 | 0.1016 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | g | | Gulf of Carpentaria, Australia | 128 | unsexed | SVL | 3.58 | 0.0001 | - | 0.881 | Survey data from AFRDC, CSIRO, NPF. |
| | h | | Mornington, northern Australia | 21 | mixed | SVL | 3.00 | 0.0013 | 0.1327 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | i | | Weipa, northern Australia | 33 | mixed | SVL | 3.00 | 0.0011 | 0.1149 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 10 | a | *Disteira kingii* | East coast, northern Australia | 2 | mixed | SVL | 3.00 | 0.0002 | 0.0150 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | b | | Gulf of Carpentaria, Australia | 27 | F | SVL | 3.09 | 0.0001 | - | 0.946 | Survey data from AFRDC, CSIRO, NPF. |
| | c | | Gulf of Carpentaria, Australia | 23 | F | SVL | 3.00 | 0.0002 | 0.0173 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | d | | Gulf of Carpentaria, Australia | 14 | M | SVL | 2.38 | 0.0046 | - | 0.810 | Survey data from AFRDC, CSIRO, NPF. |
| | e | | Gulf of Carpentaria, Australia | 12 | M | SVL | 3.00 | 0.0002 | 0.0169 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | f | | Gulf of Carpentaria, Australia | 47 | unsexed | SVL | 3.00 | 0.0002 | - | 0.899 | Survey data from AFRDC, CSIRO, NPF. |
| | g | | Mornington, northern Australia | - | mixed | SVL | 3.00 | 0.0002 | 0.0246 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | h | | Torres Strait, Australia | - | F | SVL | 3.00 | 0.0002 | 0.0233 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | i | | Weipa, northern Australia | - | mixed | SVL | 3.00 | 0.0003 | 0.0260 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 11 | a | *Disteira major* | East coast, northern Australia | 1 | M | SVL | 3.00 | 0.0050 | 0.5011 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | b | | East coast, northern Australia | - | mixed | SVL | 3.00 | 0.0006 | 0.0618 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | c | | Groote, northern Australia | - | mixed | SVL | 3.00 | 0.0006 | 0.0618 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | d | | Gulf of Carpentaria, Australia | 153 | F | SVL | 2.40 | 0.0101 | - | 0.710 | Survey data from AFRDC, CSIRO, NPF. |
| | e | | Gulf of Carpentaria, Australia | 94 | F | SVL | 3.00 | 0.0006 | 0.0553 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | f | | Gulf of Carpentaria, Australia | 84 | M | SVL | 2.64 | 0.0031 | - | 0.815 | Survey data from AFRDC, CSIRO, NPF. |

**Table A1**. Continued.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | $r^2$ | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 11 | g | *Disteira major* | Gulf of Carpentaria, Australia | 55 | M | SVL | 3.00 | 0.0005 | 0.0508 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | h | | Gulf of Carpentaria, Australia | 240 | unsexed | SVL | 2.54 | 0.0052 | - | 0.765 | Survey data from AFRDC, CSIRO, NPF. |
| | i | | northwest Australia | 3 | Unsexed | SVL | 3.00 | 0.0006 | - | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |
| | j | | northwest Australia | 1 | Female | SVL | 3.00 | 0.0007 | 0.0690 | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |
| | k | | northwest Australia | 2 | Male | SVL | 3.00 | 0.0006 | - | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |
| | l | | Torres Strait, Australia | 1 | F | SVL | 3.00 | 0.0009 | 0.0880 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | m | | Weipa, northern Australia | 17 | mixed | SVL | 3.00 | 0.0006 | 0.0579 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 12 | a | *Emydocephalus annulatus* | Gulf of Carpentaria, Australia | 1 | M | SVL | 3.00 | 0.0010 | 0.1032 | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |
| 13 | a | *Emydocephalus ijimae* | Zamamijima, Ryukyu Island | 58 | F | SVL | 2.94 | 0.0012 | - | 0.976 | Masunaga *et al.* (2003; Fig. 2 & 4). a, p. 464 & 467). |
| | b | | Zamamijima, Ryukyu Island | 52 | M | SVL | 2.53 | 0.0050 | - | 0.970 | Masunaga *et al.* (2003; Fig. 2 & 4). b, p. 464 & 466). |
| 14 | a | *Enhydrina schistosa* | Gulf of Carpentaria, Australia | 33 | F | SVL | 3.26 | 0.0002 | - | 0.922 | Survey data from AFRDC, CSIRO, NPF. |
| | b | | Gulf of Carpentaria, Australia | 24 | M | SVL | 3.15 | 0.0003 | - | 0.884 | Survey data from AFRDC, CSIRO, NPF. |
| | c | | Gulf of Carpentaria, Australia | 69 | unsexed | SVL | 3.33 | 0.0001 | - | 0.9400 | Survey data from AFRDC, CSIRO, NPF. |
| | d | | Mornington, northern Australia | - | mixed | SVL | 3.00 | 0.0006 | 0.0556 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | e | | Weipa, northern Australia | 39 | mixed | SVL | 3.00 | 0.0006 | 0.0621 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 15 | a | *Hydrophis caerulescens* | Gulf of Carpentaria, Australia | 2 | F | SVL | 3.00 | 0.0005 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. |
| | b | | Gulf of Carpentaria, Australia | 5 | M | SVL | 3.00 | 0.0057 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. |
| | c | | Gulf of Carpentaria, Australia | 7 | unsexed | SVL | 3.00 | 0.0006 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. |
| | d | | Mornington, northern Australia | 2 | M | SVL | 3.00 | 0.0005 | 0.0545 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | e | | Weipa, northern Australia | 5 | mixed | SVL | 3.00 | 0.0006 | 0.0621 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 16 | a | *Hydrophis czeblukovi* | northwestern Shelf, Australia | 1 | F | SVL | 3.00 | 0.0008 | 0.0817 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 17 | a | *Hydrophis elegans* | East coast, northern Australia | - | mixed | SVL | 3.00 | 0.0004 | 0.0353 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |

**Table A1**. Continued.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | $r^2$ | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 17 | b | *Hydrophis elegans* | Groote, northern Australia | - | mixed | SVL | 3.00 | 0.0004 | 0.0444 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | c | | Gulf of Carpentaria, Australia | 230 | F | SVL | 3.26 | 0.0001 | - | 0.898 | Survey data from AFRDC, CSIRO, NPF. |
| | d | | Gulf of Carpentaria, Australia | 231 | F | SVL | 3.00 | 0.0003 | 0.0314 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | e | | Gulf of Carpentaria, Australia | 207 | M | SVL | 3.01 | 0.0003 | - | 0.915 | Survey data from AFRDC, CSIRO, NPF. |
| | f | | Gulf of Carpentaria, Australia | 283 | M | SVL | 3.00 | 0.0003 | 0.0293 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | g | | Gulf of Carpentaria, Australia | 490 | unsexed | SVL | 3.17 | 0.0001 | - | 0.929 | Survey data from AFRDC, CSIRO, NPF. |
| | h | | Mornington, northern Australia | - | mixed | SVL | 3.00 | 0.0003 | 0.0308 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | i | | northwest Australia | 6 | Unsexed | SVL | 3.00 | 0.0003 | - | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |
| | j | | northwest Australia | 3 | Female | SVL | 3.00 | 0.0003 | - | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |
| | k | | northwest Australia | 3 | Male | SVL | 3.00 | 0.0003 | - | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |
| | l | | Weipa, northern Australia | - | mixed | SVL | 3.00 | 0.0003 | 0.0291 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 18 | a | *Hydrophis inornatus* | Gulf of Carpentaria, Australia | 1 | F | SVL | 3.00 | 0.0005 | 0.0525 | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |
| 19 | a | *Hydrophis macdowelli* | Gulf of Carpentaria, Australia | 11 | F | SVL | 3.22 | 0.0002 | - | 0.904 | Survey data from AFRDC, CSIRO, NPF. |
| | b | | Gulf of Carpentaria, Australia | 3 | M | SVL | 3.00 | 0.0005 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. Results maybe biased because N is small. |
| | c | | Gulf of Carpentaria, Australia | 14 | unsexed | SVL | 2.97 | 0.0007 | - | 0.846 | Survey data from AFRDC, CSIRO, NPF. Results maybe biased because N is small. |
| | d | | Mornington, northern Australia | 7 | mixed | SVL | 3.00 | 0.0006 | 0.0550 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | e | | northwestern Shelf, Australia | 1 | M | SVL | 3.00 | 0.0005 | 0.0478 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | f | | Weipa, northern Australia | 1 | F | SVL | 3.00 | 0.0006 | 0.0637 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 20 | a | *Hydrophis ornatus* | East coast, northern Australia | - | unsexed | SVL | 3.00 | 0.0010 | 0.1018 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | b | | Groote, northern Australia | - | mixed | SVL | 3.00 | 0.0010 | 0.0976 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | c | | Gulf of Carpentaria, Australia | 73 | F | SVL | 2.88 | 0.0016 | - | 0.640 | Survey data from AFRDC, CSIRO, NPF. |

**Table A1**. Continued.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | *r²* | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 20 | d | *Hydrophis ornatus* | Gulf of Carpentaria, Australia | 42 | F | SVL | 3.00 | 0.0008 | 0.0765 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | e | | Gulf of Carpentaria, Australia | 82 | M | SVL | 2.23 | 0.0316 | - | 0.5610 | Survey data from AFRDC, CSIRO, NPF. |
| | f | | Gulf of Carpentaria, Australia | 45 | M | SVL | 3.00 | 0.0007 | 0.0699 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | g | | Gulf of Carpentaria, Australia | 166 | unsexed | SVL | 2.51 | 0.0085 | - | 0.568 | Survey data from AFRDC, CSIRO, NPF. |
| | h | | Mornington, northern Australia | - | mixed | SVL | 3.00 | 0.0007 | 0.0701 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | i | | northwestern Shelf, Australia | 2 | M | SVL | 3.00 | 0.0008 | 0.0756 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | j | | Torres Strait, Australia | - | F | SVL | 3.00 | 0.0006 | 0.0625 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | k | | Weipa, northern Australia | - | mixed | SVL | 3.00 | 0.0007 | 0.0656 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 21 | a | *Hydrophis pacificus* | Gulf of Carpentaria, Australia | 24 | F | SVL | 3.00 | 0.0003 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. |
| | b | | Gulf of Carpentaria, Australia | 8 | M | SVL | 3.00 | 0.0004 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. |
| | c | | Gulf of Carpentaria, Australia | 32 | unsexed | SVL | 2.45 | 0.0053 | - | 0.758 | Survey data from AFRDC, CSIRO, NPF. |
| | d | | Mornington, northern Australia | 4 | mixed | SVL | 3.00 | 0.0004 | 0.0393 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 22 | a | *Lapemis hardwickii* | Darwin, northern Australia | 1 | mixed | SVL | 3.00 | 0.0016 | 0.1592 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | b | | East coast, northern Australia | 70 | mixed | SVL | 3.00 | 0.0016 | 0.1637 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | c | | Groote, northern Australia | 7 | mixed | SVL | 3.00 | 0.0013 | 0.1292 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | d | | Gulf of Carpentaria, Australia | 309 | F | SVL | 2.99 | 0.0011 | - | 0.903 | Survey data from AFRDC, CSIRO, NPF. |
| | e | | Gulf of Carpentaria, Australia | 220 | F | SVL | 3.00 | 0.0013 | 0.1297 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | f | | Gulf of Carpentaria, Australia | 175 | M | SVL | 2.82 | 0.0024 | - | 0.927 | Survey data from AFRDC, CSIRO, NPF. |
| | g | | Gulf of Carpentaria, Australia | 177 | M | SVL | 3.00 | 0.0012 | 0.1156 | - | a from c.f. of data from Ward (2000; Tab. 2, p. 158). |
| | h | | Gulf of Carpentaria, Australia | 535 | unsexed | SVL | 2.97 | 0.0012 | - | 0.933 | Survey data from AFRDC, CSIRO, NPF. |
| | i | | Mornington, northern Australia | - | mixed | SVL | 3.00 | 0.0012 | 0.1190 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| | j | | northwest Australia | 1 | Male | SVL | 3.00 | 0.0009 | - | - | a from c.f. of survey data from AFRDC, CSIRO, NPF. |

**Table A1**. Continued.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | $r^2$ | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 22 | k | *Lapemis hardwickii* | Sabah, Malaysia | 391 | F | SVL | 3.00 | 0.0016 | 0.1560 | - | a from c.f. of data from Hin *et al.* (1991; Tab. 2, p. 466). |
| | l | | Sabah, Malaysia | 363 | M | SVL | 3.00 | 0.0015 | 0.1451 | - | a from c.f. of data from Hin *et al.* (1991; Tab. 2, p. 466). |
| | m | | Weipa, northern Australia | - | mixed | SVL | 3.00 | 0.0011 | 0.1109 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 23 | a | *Laticauda colubrina* | Fiji | - | F | SVL | 2.64 | 0.0031 | 0.8150 | - | a from c.f. of data from Cogger and Heatwole (2006; Tab. 1, p. 248). |
| | b | | Fiji | - | M | SVL | 2.40 | 0.0101 | 0.7100 | - | a from c.f. of data from Cogger and Heatwole (2006; Tab. 1, p. 248). |
| | c | | Vanuatu | - | F | SVL | 2.54 | 0.0052 | 0.7650 | - | a from c.f. of data from Cogger and Heatwole (2006; Tab. 1, p. 248). |
| | d | | Vanuatu | - | M | SVL | 2.38 | 0.0046 | 0.8100 | - | a from c.f. of data from Cogger and Heatwole (2006; Tab. 1, p. 248). |
| 24 | a | *Laticauda frontalis* | unknown | - | F | SVL | 3.07 | 0.0008 | 0.8560 | - | a from c.f. of data from Cogger and Heatwole (2006; Tab. 1, p. 248). |
| | b | | unknown | 49 | M | SVL | 3.58 | 0.0001 | 0.8950 | - | a from c.f. of data from Cogger and Heatwole (2006; Tab. 1, p. 248). |
| 25 | a | *Laticauda saintgironsi* | unknown | - | F | SVL | 3.09 | 0.0001 | 0.9460 | - | a from c.f. of data from Cogger and Heatwole (2006; Tab. 1, p. 248). |
| | b | | unknown | - | M | SVL | 3.00 | 0.0002 | 0.8990 | - | a from c.f. of data from Cogger and Heatwole (2006; Tab. 1, p. 248). |
| 26 | a | *Laticauda semifasciata* | near Orchid Island, Taiwan | 70 | F | SVL | 3.00 | 0.0008 | 0.0841 | - | a from c.f. of data from Tu *et al.* (1990; Tab. 1, p. 120). |
| | b | | near Orchid Island, Taiwan | 141 | M | SVL | 3.00 | 0.0008 | 0.0775 | - | a from c.f. of data from Tu *et al.* (1990; Tab. 1, p. 120). |
| 27 | a | *Pelamis platurus* | Gulf of Carpentaria, Australia | 2 | F | SVL | 3.00 | 0.0008 | - | - | a from mean c.f. of survey data from AFRDC, CSIRO, NPF. |
| | b | | Weipa, northern Australia | 2 | F | SVL | 3.00 | 0.0008 | 0.0807 | - | a from c.f. of data from Fry *et al.* (2001; Tab. 2, p. 59). |
| 28 | a | *Amblyrhynchus cristatus* (Squamata, Iguanidae) | Genovesa, Galapagos Island | 41 | M | SVL | 3.00 | 0.0458 | 4.579 | - | a from c.f. of territorial males from Wikelski *et al.* (1996; Tab. 1, p. 587). |
| | b | | Genovesa, Galapagos Island | 15 | M | SVL | 3.00 | 0.0424 | 4.244 | - | a from c.f. of marginal males from Wikelski *et al.* (1996; Tab. 1, p. 587). |

**Table A1**. Continued.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | $r^2$ | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 28 | c | *Amblyrhynchus cristatus* | Genovesa, Galapagos Island | 16 | M | SVL | 3.00 | 0.0458 | 4.578 | - | a from c.f. of small males from Wikelski *et al.* (1996; Tab. 1, p. 587). |
|  | d |  | Genovesa, Galapagos Island | 11 | M | SVL | 3.00 | 0.0448 | 4.476 | - | a from c.f. of single territories from Wikelski *et al.* (1996; Tab. 3, p. 589). |
|  | e |  | Genovesa, Galapagos Island | 30 | M | SVL | 3.00 | 0.0463 | 4.628 | - | a from c.f. of leks from Wikelski *et al.* (1996; Tab. 3, p. 589). |
| 29 | a | *Caretta caretta*<br>(Testudines, Cheloniidae) | Curacao | 23 | unsexed | SCL | 2.95 | 0.1655 | - | 0.986 | Nagelkerken *et al.* (2003; Tab. 1, p. 186). Not a good representative of the population. |
|  | b |  | USA (Cheasapeake, Florida), UK, France, Japan | 431 | unsexed | SCL | 2.82 | 0.000282 |  | 0.970 | Wabnitz (2008; Tab. 1 p. xx); weight in kg. |
| 30 | a | *Chelonia mydas* | Gulf coast of Florida, USA | 208 | unsexed | CL | 2.91 | 0.1674 | - | 0.993 | Carr & Cadwell (1956; Tab. 2, p. 15). |
|  | b |  | Saurashtra Coast, Gujarat, India | 69 | unsexed | CCL | 3.00 | 0.1145 | 11.45 | - | a from c.f. of data from Kannan *et al.* (2005; Tab. 2, p. 5). |
|  | c |  | USA (Florida), Mexico (Baja California), Tortuguero, Ascension, Suriname, | 426 | unsexed | SCL | 2.90 | 0.000206 |  | 0.990 | Wabnitz (2008; Tab. 1 p. xx); weight in kg. |
| 31 | a | *Eretmochelys imbricata* | Baja California, Mexico | 200 | unsexed | SCL | 3.00 | 0.1519 | 14.99 | - | Seminoff *et al.* (2003; p. 1355). |
|  | b |  | Milman, Great Barrier Reef, Australia | - | F | CCL | 3.00 | 0.0922 | 9.224 | - | Loop *et al.* (1995; Tab. 2, p. 247). |
|  | c |  | Persian Gulf (Shidvar, Ommolkaran, Nakhillo and Queshm Islands), Iran | 25 | unsexed | CCL | 2.96 | 0.1275 | - | 0.844 | Morabaki & Elmi (2005; Tab. 1, p. 7). |
|  | d |  | Honduras, Cayman, Barbados, Suriname | 112 | unsexed | SCL | 2.74 | 0.000278 |  | 0.990 | Wabnitz (2008; Tab. 1 p. xx); weight in kg. |
| 32 | a | *Lepidochelys kempi* | Florida, USA | 78 | unsexed | CL | 2.49 | 0.8919 | - | 0.951 | Carr & Cadwell (1956; Tab. 2, p. 15). |
|  | b |  | USA (Cheasapeake, Florida), UK, France | 145 | unsexed | SCL | 2.84 | 0.000247 |  | 0.960 | Wabnitz (2008; Tab. 1 p. xx); weight in kg. |
| 33 | a | *Lepidochelys olivacea* | Northern Territory, Australia | 85 | F | CCL | 3.00 | 0.0001 | 0.0111 | - | a from c.f. of data from Whiting *et al.* (2007; Tab. 3, p. 205); weight in kg. |
|  | b |  | Primeira Islands, Mocambique | 1 | unsexed | CL | 3.00 | 0.1166 | 11.66 | - | a from c.f. of data from Hughes (1972; Tab. 1, p. 129). |
|  | c |  | Hawaii, Brazil, Suriname, Mozambique | 40 | unsexed | SCL | 2.68 | 0.000479 |  | 0.840 | Wabnitz (2008; Tab. 1 p. xx); weight in kg. |
| 34 | a | *Natator depressus* | Field Island, Australia | 205 | unsexed | CCL | 3.00 | 0.0001 | 0.0105 | - | a from c.f. of data from Schäuble *et al.* (2006; Tab. 2, p. 192); weight in kg. |
| 35 | a | *Dermochelys coriacea*<br>(Testudines, Dermochelydae) | Florida, USA | 2 | unsexed | SCL | 3.00 | 0.0897 | - | - | a from mean c.f. of data from Jones *et al.* (2008; Tab. 3). |
|  | b |  | Nova Scotia, Canada | 16 | unsexed | CCL | 3.67 | 0.0044 | - | 0.853 | James *et al.* (2007; Fig. 3, p. 248). |
|  | c |  | St. Croix, US Virgin islands | 102 | F | CCL | 2.41 | 1.8253 | - | 0.746 | James *et al.* (2005; Fig. 3, p. 199). |

**Table A1**. Continued.

| Spec. No. | Stock No. | Species | Locality | n | Sex | Type | *b* | *a* | *c.f.* | $r^2$ | Method/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 35 | d | *Dermochelys coriacea* | University of British Colombia, Vancouver, Canada | 101 | unsexed | SCL | 2.81 | 0.2640 | - | - | Jones *et al.* (2008; Tab. 3). |
| | e | | Unknown, American Samoa | 1 | unsexed | SCL | 3.00 | 0.1180 | 11.80 | - | a from c.f. of data from Jones *et al.* (2008; Tab. 3). |
| | f | | Unknown, Hawaii | 3 | unsexed | SCL | 3.00 | 0.1149 | - | - | a from mean c.f. of data from Jones *et al.* (2008; Tab. 3). |
| | g | | Unknown | 1 | unsexed | SCL | 3.00 | 0.1118 | 11.18 | - | a from c.f. of data from Jones *et al.* (2008; Tab. 3). |
| | h | | western Australia, Australia | 2 | unsexed | SCL | 3.00 | 0.0656 | - | - | a from mean c.f. of data from Jones *et al.* (2008; Tab. 3). |

**Table A2**. Growth parameter estimates assembled for marine reptiles and used to obtain Figure 2. Sex: U=unsexed or mixed; F=females; M=males. Type: TL=total length; SVL=snout-vent length; SCL=straight carapace length; CCL=curved carapace length; CL=carapace length.

| Spec. No. | Stock No. | Species | Locality | N | Sex | $L_\infty$ cm | Type | $W_\infty$ kg | $Z/K$ (or $Z$) | K years$^{-1}$ | Φ' | K from Φ' | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | a | *Crocodylus porosus* (Crocodilia, Crocodylidae) | N. Territory, Australia | 7665 | U | 323.1 | TL | 144 | - | 0.710 | 4.87 | - | L∞ & K from length frequency analysis of data from Messel and Vorlicek (1986; Tab. 1a, p. 76-84). Unexploited; 61-305 cm. W∞ from Tab 1 (1a). |
|  | b |  | Queensland, Australia | 907 | U | 265.2 | TL | 70.5 | - | 2.500 | 5.25 | - | L∞ & K from length frequency analysis of data from Messel and Vorlicek (1986; Tab. 1a, p. 76-84). Unexploited; 61-244 cm. W∞ from Tab 1 (1a). |
|  | c |  | W. Australia | 736 | U | 262.1 | TL | 67.6 | - | 0.750 | 4.71 | - | L∞ & K from length frequency analysis of data from Messel and Vorlicek (1986; Tab. 1a, p. 76-84). Unexploited; 61-244 cm. W∞ from Tab 1 (1a). |
| 2 | a | *Acrochordus granulatus* (Squamata, Acrochordidae) | Phangnga Bay, Thailand | 77 | F | 93.4 | SVL | 0.425 | 4.04 | - | - | 0.829 | L∞ from single length frequency histogram from Wangkulangkul *et al.* (2005; Fig. 2, p. 260). Exploited; 35-81 cm. W∞ from Tab 1 (2a). K=ave. Φ'; all sea snakes. |
|  | b |  | Phangnga Bay, Thailand | 42 | M | 72.2 | SVL | 0.145 | 1.61 | - | - | 1.386 | L∞ from single length frequency histogram from Wangkulangkul *et al.* (2005; Fig. 2, p. 259). Exploited 35-65 cm. W∞ from Tab 1 (2b). K=ave. Φ'; all sea snakes. |
| 3 | a | *Cerberus rynchops* (Squamata, Colubridae) | Muar River, Malaysia | 181 | U | 85.0 | SVL | 0.360 | (0.99) | 0.270 | 3.29 | - | L∞ & K from length frequency analysis of data from Jayne *et al.* (1988; Tab. 1, p. 5 rows 1-2). Unexploited; 24-64 cm. W∞ from Tab 1 (3a). |
|  | b |  | Muar River, Malaysia | 597 | U | 76.8 | SVL | 0.265 | (1.53) | 0.410 | 3.38 | - | L∞ & K from length frequency analysis of data from Jayne *et al.* (1988; Tab. 1, p. 5 rows 3-6). Unexploited; 1984-1987; 24-64 cm. W∞ from Tab 1 (3a). |
| 4 | a | *Acalyptophis peronii* (Squamata, Hydrophiidae) | G. Carpentaria, Australia | 50 | U | 137.7 | SVL | 1.79 | 3.29 | - | - | 0.382 | L∞ from single length frequency histogram from FRDC/CSIRO/NPF survey data. Exploited; 70-126 cm. W∞ from Tab 1 (4e). K=ave. Φ' Hydrophiidae. |
| 5 | a | *Aipysurus duboisii* | G. Carpentaria, Australia | 20 | U | 114.6 | SVL | 0.796 | 0.990 | - | - | 0.551 | L∞ from single length frequency histogram from FRDC/CSIRO/NPF survey data. Exploited; 80-110 cm. W∞ from Tab 1 (6e). K=ave. Φ'; Hydrophiidae. |
| 6 | a | *Aipysurus eydouxii* | G. Carpentaria, Australia | 106 | U | 112.8 | SVL | 1.32 | 3.05 | - | - | 0.569 | L∞ from single length frequency histogram from FRDC/CSIRO/NPF survey data. Exploited; 35-96 cm. W∞ from Tab 1 (7g). K=ave. Φ'; Hydrophiidae. |

**Table A2**. Continued.

| Spec. No. | Stock No. | Species | Locality | N | Sex | $L_\infty$ cm | Type | $W_\infty$ kg | *Z/K* (or *Z*) | *K* years$^{-1}$ | *Φ'* | *K* from *Φ'* | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 7 | a | *Aipysurus laevis* | G. Carpentaria, Australia | 74 | U | 138.8 | SVL | 4.00 | 2.16 | - | - | 0.375 | $L_\infty$ from single L/F histogram; FRDC/CSIRO/NPF survey data. Exploited; 60-130cm. $W_\infty$ from Tab 1 (8g). K=ave. Φ'; Hydrophiidae. |
| 8 | a | *Astrotia stokesii* | G. Carpentaria, Australia | 131 | U | 180.1 | SVL | 10.0 | 0.020 | - | - | 0.223 | $L_\infty$ from single L/F histogram; FRDC/CSIRO/NPF survey data. Exploited; 55-176 cm. $W_\infty$ from Tab 1 (9g). K=ave. Φ'; Hydrophiidae. |
| 9 | a | *Disteira kingii* | G. Carpentaria, Australia | 48 | U | 174.2 | SVL | 1.07 | 2.44 | - | - | 0.239 | $L_\infty$ from single L/F histogram; FRDC/CSIRO/NPF survey data. Exploited; 60-170 cm. $W_\infty$ from Tab 1 (10f). K=ave. Φ'; Hydrophiidae. |
| 10 | a | *Disteira major* | G. Carpentaria, Australia | 248 | U | 176.4 | SVL | 2.63 | 1.23 | - | - | 0.233 | $L_\infty$ from single L/F histogram; FRDC/CSIRO/NPF survey data. Exploited; 60-160 cm. $W_\infty$ from Tab 1 (11h). K=ave. Φ'; Hydrophiidae. |
| 11 | a | *Emydocephalus ijimae* | Zamamijima, Ryukyu Island | - | F | 79.8 | SVL | 0.449 | - | 3.820 | 4.39 | - | Direct fitting of VBGF to age at length from Masunaga and Ota (2003; Fig. (2,4)a, p. 464,467); $t_0$= 0; unexploited; 42-83 cm. $W_\infty$ from Tab 1 (13a). |
|  | b |  | Zamamijima, Ryukyu Island | - | M | 66.8 | SVL | 0.210 | - | 2.540 | 4.05 | - | Direct fitting of VBGF to age at length from Masunaga and Ota (2003; Fig. (2,4)b, p. 464 & 466). $t_0$=-0.42; unexploited; 30-68 cm. $W_\infty$ from Tab 1 (13b). |
| 12 | a | *Enhydrina schistosa* | G. Carpentaria, Australia | 69 | U | 102.1 | SVL | 0.628 | 1.38 | - | - | 0.752 | $L_\infty$ from single L/F histogram from FRDC/CSIRO/NPF survey data. Exploited; 35-96 cm. $W_\infty$ from Tab 1(14c). K=ave. Φ'; same species. |
|  | b |  | Muar, Malaysia | 295 | F | 113.9 | SVL | 0.890 | (1.13) | 0.600 | 3.89 | - | $L_\infty$ & K from L/F analysis of data from Voris and Jayne (1979; Fig. 1(b,d,f,h), p. 311). Exploited; 21-102 cm. $W_\infty$ from Tab 1 (14a). |
|  | c |  | Muar, Malaysia | 359 | M | 103.4 | SVL | 0.583 | (1.52) | 0.740 | 3.90 | - | $L_\infty$ & K from L/F analysis of data from Voris and Jayne (1979; Fig. 1(a,c,e,g), p. 310). Exploited; 21-100 cm. $W_\infty$ from Tab 1 (14b). |
| 13 | a | *Hydrophis elegans* | Australian continental shelf | 306 | M | 170.1 | SVL | 1.33 | - | 0.310 | 3.95 | - | VBGF parameters from Ward (2001; Tab. 3, p. 196); $t_0$=-0.93; T=28-29°C; exploited; 75-193 cm. $W_\infty$ from Tab 1 (17e). |
|  | b |  | Australian continental shelf | 276 | F | 221.3 | SVL | 3.09 | - | 0.170 | 3.92 | - | VBGF parameters from Ward (2001; Tab. 3, p. 196); $t_0$=-2.1; T=28-29°C; exploited; 82-218 cm. $W_\infty$ from Tab 1 (17c). |
|  | c |  | G. Carpentaria, Australia | 525 | U | 257.0 | SVL | 5.01 | (0.590) | 0.170 | 4.05 | - | $L_\infty$ & K from L/F analysis; FRDC/CSIRO/NPF survey data. Exploited; 40-221 cm. $W_\infty$ from Tab 1 (17g). |

**Table A2**. Continued.

| Spec. No. | Stock No. | Species | Locality | N | Sex | $L_\infty$ cm | Type | $W_\infty$ kg | Z/K (or Z) | K years$^{-1}$ | Φ' | K from Φ' | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 14 | a | *Hydrophis ornatus* | G. Carpentaria, Australia | 178 | U | 129.4 | SVL | 1.70 | 1.40 | - | - | 0.432 | $L_\infty$ from single L/F histogram from FRDC/CSIRO/NPF survey data. Exploited; 60-120 cm. $W_\infty$ from Tab 1 (20g). K=ave. Φ';*Hydrophis*. |
| 15 | a | *Hydrophis pacificus* | G. Carpentaria, Australia | 32 | U | 188.8 | SVL | 2.01 | 1.42 | - | - | 0.203 | $L_\infty$ from single L/F histogram from FRDC/CSIRO/NPF survey data. Exploited; 120-180 cm. $W_\infty$ from Tab 1 (21c). K=ave. Φ'; *Hydrophis*. |
| 16 | a | *Lapemis hardwickii* | Australian continental shelf | 227 | F | 112.2 | SVL | 1.51 | - | 0.410 | 3.71 | - | VBGF parameters from Ward (2001; Tab. 3, p. 196); $t_0$=-0.86; exploited; 42-120 cm. $W_\infty$ from Tab 1 (22d). |
| | b | | Australian continental shelf | 184 | M | 113.0 | SVL | 1.48 | - | 0.440 | 3.75 | - | VBGF parameters from Ward (2001; Tab. 3, p. 196); $t_0$=-0.57; exploited; 50-126 cm. $W_\infty$ from Tab 1 (22f). |
| | c | | G. Carpentaria, Australia | 549 | U | 132.0 | SVL | 2.45 | (2.98) | 0.750 | 4.12 | - | $L_\infty$ & K from L/F analysis of data from FRDC/CSIRO/NPF survey data. Exploited; 30-121 cm. $W_\infty$ from Tab 1 (22h). |
| | d | | Sabah, Malaysia | 391 | F | 94.4 | SVL | 1.31 | 3.06 | - | - | 0.812 | $L_\infty$ from single L/F histogram from Hin *et al.* (1991; Fig. 1, p. 467). Exploited; 30-80 cm. $W_\infty$ from Tab 1 (22k). K=ave. Φ'; same species. |
| | e | | Sabah, Malaysia | 363 | M | 86.2 | SVL | 0.929 | 2.38 | - | - | 0.974 | $L_\infty$ from single L/F histogram from Hin *et al.* (1991; Fig. 1, p. 468). Exploited; 34-84 cm. $W_\infty$ from Tab 1 (22l). K=ave. Φ'; same species. |
| 17 | a | *Laticauda colubrina* | Indo-Pacific | - | F | 170.4 | SVL | 2.39 | 2.55 | - | - | 0.249 | $L_\infty$ from single L/F histogram from Heatwole *et al.* (2005; Fig. 24, p. 44). Exploited; 25-156 cm. $W_\infty$ from Tab 1 (23a). K=ave. Φ'; Hydrophiidae. |
| | b | | Indo-Pacific | - | M | 136.6 | SVL | 1.34 | 1.89 | - | - | 0.388 | $L_\infty$ from single L/F histogram from Heatwole *et al.* (2005; Fig. 24, p. 44). Exploited; 30-125 cm. $W_\infty$ from Tab 1 (23b). K=ave. Φ'; Hydrophiidae. |
| | c | | Indo-Pacific | 1294 | U | 125.8 | SVL | 0.454 | 1.47 | - | - | 0.457 | $L_\infty$ from single L/F histogram from Heatwole *et al.* (2005; Fig. 24, p. 44). Exploited; 15-165 cm. $W_\infty$ from Tab 1 (23d). K=ave. Φ'; Hydrophiidae. |
| | d | | Mabualau and Toberua, Fiji | 352 | F | 150.8 | SVL | 1.73 | 2.97 | - | - | 0.318 | $L_\infty$ from single L/F histogram from Shetty and Shine (2002; Fig. 1b, p. 48). Unexploited; 30-140 cm. $W_\infty$ from Tab 1 (23a). K=ave. Φ'; Hydrophiidae. |
| | e | | Mabualau and Toberua, Fiji | 648 | M | 90.8 | SVL | 0.504 | 0.763 | - | - | 0.878 | $L_\infty$ from single L/F histogram from Shetty and Shine (2002; Fig. 1a, p. 48). Unexploited; 30-91 cm. $W_\infty$ averaged from Tab 1 (23b). K=ave. Φ; Hydrophiidae. |

**Table A2**. Continued.

| Spec. No. | Stock No. | Species | Locality | N | Sex | $L_\infty$ cm | Type | $W_\infty$ kg | Z/K (or Z) | K years$^{-1}$ | Φ' | K from Φ' | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 18 | a | *Laticauda saintgironsi* | Indo-Pacific | - | F | 122.7 | SVL | 0.359 | 1.68 | - | - | 0.480 | $L_\infty$ from single L/F histogram from Heatwole *et al.* (2005; Fig. 25, p. 45). Exploited; 30-111 cm. $W_\infty$ from Tab 1 (25a). K=ave. Φ'; Hydrophiidae. |
| | b | | Indo-Pacific | - | M | 96.5 | SVL | 1.82 | 4.44 | - | - | 0.776 | $L_\infty$ from single L/F histogram from Heatwole *et al.* (2005; Fig. 25, p. 45). Exploited; 35-86 cm. $W_\infty$ from Tab 1 (25b). K=ave. Φ'; Hydrophiidae. |
| | c | | Indo-Pacific | 192 | U | 130.6 | SVL | 0.443 | 1.38 | - | - | 0.424 | $L_\infty$ from single L/F histogram from Heatwole *et al.* (2005; Fig. 25, p. 45). Exploited; 20-120 cm. $W_\infty$ averaged from Tab 1 (25a and b). K=ave. Φ'; Hydrophiidae. |
| 19 | a | *Amblyrhynchus cristatus* (Squamata, Iguanidae) | Genovesa, Galapagos Island | 41 | M | 28.6 | SVL | 1.08 | 1.24 | - | - | 1.516 | $L_\infty$ from single L/F histogram from Wikelski *et al.* (1996; Fig. 6, p. 590). Unexploited; territorial males; 21-29 cm $W_\infty$ from Tab 1 (28a). K=Φ'; same species. |
| | b | | Genovesa, Galapagos Island | 318 | U | 29.8 | SVL | 1.12 | (4.83) | 1.400 | 3.09 | - | $L_\infty$ & K from L/F analysis of data from Wikelski and Trillmich (1997; Fig. 8, p. 928). Unexploited; 11-27 cm; narrow size range may not be a good representative of the population. $W_\infty$ from Tab 1 (28b). |
| | c | | Sta.Fe, Galapagos Island | 8000 | U | 41.1 | SVL | 3.17 | 1.76 | - | - | 0.737 | $L_\infty$ from single L/F histogram from Wikelski and Trillmich (1997; Fig. 2, p. 926). Unexploited; 11-37 cm. $W_\infty$ from Tab 1 (28c). K=Φ'; same species. |
| 20 | a | *Caretta caretta* (Testudines, Cheloniidae) | Azores | 1600 | U | 73.4 | SCL | 55.5 | 2.09 | - | - | 0.102 | $L_\infty$ from single L/F histogram from Bjorndal *et al.* (2003; Tab. 1, p. 735). Unexploited; 10-70 cm. $W_\infty$ from Tab 1 (29b). K=ave. Φ'; same species. |
| | b | | Florida, Georgia, S. Carolina, USA | 118 | U | 110.0 | SCL | 175 | - | 0.031 | 2.58 | - | VBGF parameters from Epperly *et al.* (2001; Tab. 8 p. 46). Unexploited; 45-110 cm; mark-recapture. $W_\infty$ from Tab 1 (29b). |
| | c | | Cayman Islands | 250 | U | 110.3 | SCL | 174 | 1.34 | - | - | 0.048 | $L_\infty$ from single L/F histogram from Epperly and Teas (2002; Tab. 1, p. 468). Unexploited; 1-101 cm. $W_\infty$ from Tab 1 (29b). K=ave. Φ'; same species. |
| | d | | Florida, USA | 1234 | U | 110.9 | SCL | 178 | - | 0.044 | 2.79 | - | VBGF parameters from Bjorndal *et al.* (2001; Fig. 1, p. 242). Unexploited; stranded sea turtles; 46-87 cm. $W_\infty$ from Tab 1 (29b). |
| | e | | Florida, USA | 41 | U | 94.7 | SCL | 114 | - | 0.115 | 3.01 | - | VBGF parameters from Epperly *et al.* (2001; Tab. 8 p. 46). Unexploited; 53-77 cm; mark-recapture. $W_\infty$ from Tab 1 (29b). |
| | f | | Florida, USA | 51 | U | 96.1 | SCL | 119 | - | 0.059 | 2.73 | - | VBGF parameters from Epperly *et al.* (2001; Tab. 8 p. 46). Unexploited; 38-110 cm; mark-recapture. $W_\infty$ from Tab 1 (29b). |

**Table A2**. Continued.

| Spec. No. | Stock No. | Species | Locality | N | Sex | *$L_\infty$* cm | Type | *$W_\infty$* kg | *Z/K* (or *Z*) | *K* years$^{-1}$ | *Φ'* | *K* from *Φ'* | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 20 | g | *Caretta caretta* | Florida, USA | 19 | U | 96.1 | SCL | 119 | - | 0.057 | 2.72 | - | VBGF parameters from Epperly *et al.* (2001; Tab. 8 p. 46). Unexploited population; 28-110 cm; mark-recapture. $W_\infty$ from Tab 1 (29b). |
| | h | | G. Mexico, USA | 570 | U | 105.7 | SCL | 155 | - | 0.051 | 2.81 | - | VBGF parameters from Bjorndal *et al.* (2001; Fig. 2, p. 243). Unexploited; stranded sea turtles; 46-87 cm. $W_\infty$ from Tab 1 (29b). |
| | i | | G. Mexico, USA | 1639 | U | 125.1 | SCL | 250 | 3.32 | - | - | 0.037 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 6-7, p. 16-18). Unexploited; 0-121 cm. $W_\infty$ from Tab 1 (29b). K=ave. Φ'; same species. |
| | j | | N. Carolina, USA | 57 | U | 106.9 | SCL | 160 | - | 0.052 | 2.77 | - | VBGF parameters from Epperly *et al.* (2001; Tab. 8 p. 46). Unexploited; with 45-76 cm; mark-recapture. $W_\infty$ from Tab 1 (29b). |
| | k | | S.E. USA | 54 | U | 96.7 | SCL | 121 | - | 0.064 | 2.78 | - | VBGF parameters from Epperly *et al.* (2001; Tab. 8 p. 46). Unexploited; 62-104 cm; mark-recapture. $W_\infty$ from Tab 1 (29b). |
| | l | | W. Atlantic | 6727 | U | 120.0 | SCL | 222 | 2.57 | - | - | 0.041 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 5-7, p. 14-18). Unexploited; 0-121 cm. $W_\infty$ from Tab 1 (29b). K=ave. Φ'; same species. |
| 21 | a | *Chelonia mydas* | Alagadi beach, Cyprus | 92 | F | 101.1 | SCL | 127 | 1.78 | - | - | 0.083 | $L_\infty$ from single L/F histogram from Broderick *et al.* (2003; Fig. 2a, p. 98). Growth rate: 11 cm CCL year$^{-1}$; 0.27 cm CCW year$^{-1}$; unexploited; 76-106 cm. $W_\infty$ from Tab 1 (30c). K=ave. Φ'; same species. |
| | b | | Bahia Magdalena, Mexico | 718 | U | 102.5 | SCL | 132 | 2.60 | - | - | 0.094 | $L_\infty$ from single L/F histogram from Koch *et al.* (2006; Fig. 3, p. 331). Unexploited; juveniles; 35-91 cm. $W_\infty$ from Tab 1 (30c). K=ave. Φ'; same species. |
| | c | | Bahia Magdalena, Mexico | 212 | U | 101.0 | SCL | 127 | (0.160) | 0.040 | 2.61 | - | Seasonalized VBGF parameters C= 0, $t_s$= 0.75, $t_0$= 0 from Koch *et al.* (2007; p. 35). Unexploited; 43-73 cm. Growth 3x higher in summer (0.28 cm month$^{-1}$) than winter 0.09 cm month$^{-1}$; ave. growth rate 1.62 cm year$^{-1}$. $W_\infty$ from Tab 1 (30c). |
| | d | | Baja California, Mexico | 200 | U | 106.1 | SCL | 146 | 2.87 | - | - | 0.088 | $L_\infty$ from single L/F histogram from Seminoff *et al.* (2003; Fig. 4, p. 1359). Unexploited; 46-100 cm. $W_\infty$ from Tab 1 (30c). K= ave. Φ' for same species. |
| | e | | Cayman Islands | 176 | U | 88.2 | SCL | 85.8 | 0.704 | - | - | 0.127 | $L_\infty$ from single L/F histogram from Epperly and Teas (2002; Tab. 1, p. 468). Unexploited; 1-81 cm. $W_\infty$ from Tab 1 (30c). K=ave. Φ'; same species. |

**Table A2**. Continued.

| Spec. No. | Stock No. | Species | Locality | N | Sex | $L_\infty$ cm | Type | $W_\infty$ kg | Z/K (or Z) | K years$^{-1}$ | $\Phi'$ | K from $\Phi'$ | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 21 | f | *Chelonia mydas* | Pamlico, N. Carolina, USA | 226 | U | 87.7 | SCL | 84.4 | (0.760) | 0.320 | 3.39 | - | $L_\infty$ & K from L/F analysis of data from Epperly *et al.* (2007; Fig. 6, p. 590). Unexploited; 20-80 cm. $W_\infty$ from Tab 1 (30c). |
| | g | | Great Inagua, Bahamas | 964 | U | 98.3 | SCL | 117 | - | 0.740 | 3.85 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992; 26-72 cm. $W_\infty$ from Tab 1 (30c). |
| | h | | Great Inagua, Bahamas | 884 | U | 98.3 | SCL | 117 | - | 0.074 | 2.85 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992. $W_\infty$ from Tab 1 (30c). |
| | i | | Great Inagua, Bahamas | 839 | U | 99.4 | SCL | 121 | - | 0.072 | 2.85 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992. $W_\infty$ from Tab 1 (30c). |
| | j | | Great Inagua, Bahamas | 772 | U | 92.6 | SCL | 98.7 | - | 0.082 | 2.85 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992. $W_\infty$ from Tab 1 (30c). |
| | k | | Great Inagua, Bahamas | 691 | U | 168.0 | SCL | 554 | - | 0.025 | 2.85 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992. $W_\infty$ from Tab 1 (30c). |
| | l | | Great Inagua, Bahamas | 571 | U | 82.2 | SCL | 69.9 | - | 0.122 | 2.92 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992. $W_\infty$ from Tab 1 (30c). |
| | m | | Great Inagua, Bahamas | 509 | U | 158.6 | SCL | 469 | - | 0.035 | 2.94 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992. $W_\infty$ from Tab 1 (30c). |
| | n | | Great Inagua, Bahamas | 363 | U | 162.8 | SCL | 506 | - | 0.033 | 2.94 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992. $W_\infty$ from Tab 1 (30c). |
| | o | | Great Inagua, Bahamas | 211 | U | 84.4 | SCL | 75.5 | - | 0.114 | 2.91 | - | VBGF parameters from Bjorndal *et al.* (1995; Tab. 1, p. 74). Unexploited; 1983-1992. $W_\infty$ from Tab 1 (30c). |
| | p | | Gulf of Mexico, USA | 357 | U | 96.5 | SCL | 111 | 0.611 | - | - | 0.106 | $L_\infty$ from single L/F histogram from Teas (1993; tab. 9-10, p. 22-24). Unexploited; 0-91 cm. $W_\infty$ from Tab 1 (30c). K=ave. Φ'; same species. |
| | q | | Queensland, Australia | 94 | U | 98.8 | SCL | 119 | 0.628 | - | - | 0.087 | $L_\infty$ from single L/F histogram from Robins (2007; Fig. 2, p. 163). Exploited; 20-101 cm. $W_\infty$ from Tab 1 (30c). K=ave. Φ'; same species. |
| | r | | Watamu, Kenya | 1666 | U | 110.3 | SCL | 164 | - | 0.070 | 2.98 | - | Direct fitting of VBGF to age at length from Watson (2006; Fig. 5.7, p. 45). Unexploited; 33-115 cm; $t_0$=-0.75; growth rates 0.468-10.67 cm (CCL) year$^{-1}$, average growth 5.18 cm year$^{-1}$. $W_\infty$ from Tab 1 (30c). |

**Table A2**. Continued.

| Spec. No. | Stock No. | Species | Locality | N | Sex | $L_\infty$ cm | Type | $W_\infty$ kg | Z/K (or Z) | K years$^{-1}$ | Φ' | K from Φ' | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 21 | s | *Chelonia mydas* | W. Atlantic | 1393 | U | 118.8 | SCL | 203 | 1.73 | - | - | 0.070 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 8-10, p. 20-24). Unexploited; 0-111 cm. $W_\infty$ from Tab 1 (30c). K=ave. Φ'; same species. |
|  | t |  | Yaeyama, Okinawa, Japan | 50 | U | 88.8 | SCL | 87.4 | 1.84 | - | - | 0.126 | $L_\infty$ from single L/F histogram from Sakai *et al.* (2000; Fig. 2a, p. 379). Exploited; 32-81 cm. $W_\infty$ from Tab 1 (30c). K=ave. Φ'; same species. |
| 22 | a | *Chelonia mydas agassizii* | Bahia Magdalena, Mexico | 52 | U | 100.0 | SCL | 123 | - | - | 2.70 | 0.050 | VBGF parameters from Lyons *et al.* (2002; Fig. 2). C=0.65, $t_s$=0.72; unexploited; 43-72 cm; mark-recapture. $W_\infty$ from Tab 1 (30c). |
| 23 | a | *Eretmochelys imbricata* | Great Barrier Reef, Australia | 106 | U | 85.7 | SCL | 58.3 | 1.82 | - | - | 0.119 | $L_\infty$ from single L/F histogram from Limpus (1992; Fig. 4, p. 498). Unexploited; 35-88 cm. $W_\infty$ from Tab 1 (31d). K=ave. Φ'; Cheloniidae. |
|  | b |  | Cuban Archipelago | 6789 | F | 99.0 | SCL | 89.6 | 2.01 | - | - | 0.101 | $L_\infty$ from single L/F histogram from Moncada *et al.* (1999; Tab. 1, p. 258). Unexploited; 31-92 cm. $W_\infty$ from Tab 1 (31b). K=ave. Φ'; Cheloniidae. |
|  | c |  | G. Mexico, USA | 117 | U | 61.7 | SCL | 35.7 | 2.71 | - | - | 0.260 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 15-16, p. 34-36). Unexploited; juveniles; 0-50 cm. $W_\infty$ from Tab 1 (31a). K=ave. Φ'; Cheloniidae. |
|  | d |  | NeedHam's Point, Barbados | 1310 | F | 99.4 | SCL | 90.7 | 1.39 | - | - | 0.089 | $L_\infty$ from single L/F histogram from Beggs *et al.* (2007; Fig. 3, p. 162). Unexploited; 77-103 cm. $W_\infty$ from Tab 1 (31b). K=ave. Φ'; Cheloniidae. |
|  | e |  | W. Atlantic | 169 | U | 86.0 | SCL | 58.9 | 1.61 | - | - | 0.134 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 14-16, p. 32-36). Unexploited; 0-81 cm. $W_\infty$ from Tab 1 (31d). K=ave. Φ'; Cheloniidae. |
| 24 | a | *Lepidochelys kempii* | Cape Canaveral, Florida, USA | 147 | U | 66.2 | SCL | 31.1 | (3.09) | 1.30 | 3.76 | - | $L_\infty$ from single L/F histogram from Schmid (2000; Fig. 1-3, p. 10). Unexploited; 20-60 cm. $W_\infty$ from Tab 1 (32a). |
|  | b |  | Cayman Islands | 631 | U | 61.5 | SCL | 23.5 | 1.22 | - | - | 0.408 | $L_\infty$ from single L/F histogram from Epperly and Teas (2002; Tab. 1, p. 468). Unexploited; 1-51 cm. $W_\infty$ from Tab 1 (32b). K=ave. Φ'; same species. |
|  | c |  | Cedar Keys, USA | 253 | U | 61.1 | SCL | 23.1 | 1.22 | - | - | 0.413 | $L_\infty$ from single L/F histogram from Schmid (2000; Fig. 1-3, p. 10). Unexploited; 25-60 cm. $W_\infty$ from Tab 1 (32b). K=ave. Φ'; same species. |
|  | d |  | Chesapeake Bay, USA | 38 | U | 61.6 | SCL | 23.6 | 1.86 | - | - | 0.406 | $L_\infty$ from single L/F histogram from Schmid (2000; Fig. 1-3, p. 10). Unexploited; 20-56 cm. $W_\infty$ from Tab 1 (32b). K=ave. Φ'; same species. |
|  | e |  | E. Pamlico, N. Carolina, USA | 67 | U | 61.6 | SCL | 23.5 | (0.720) | 0.770 | 3.46 | - | $L_\infty$ & K from L/F analysis of data from Epperly *et al.* (2007; Fig. 7, p. 288). Unexploited; 25-59 cm. $W_\infty$ from Tab 1 (32b). |

**Table A2**. Continued.

| Spec. No. | Stock No. | Species | Locality | N | Sex | $L_\infty$ cm | Type | $W_\infty$ kg | $Z/K$ (or $Z$) | $K$ years$^{-1}$ | $\Phi'$ | $K$ from $\Phi'$ | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 24 | f | *Lepidochelys kempii* | Florida, USA | 36 | U | 69.4 | SCL | 33.0 | - | 0.129 | 2.79 | - | VBGF parameters from Coyne (2000; Tab. 4, p. 59). Unexploited; recaptured wild and head-start turtles; $W_\infty$ from Tab 1 (32a). |
| | g | | G. Mexico, USA | 114 | U | 62.3 | SCL | 24.3 | - | 0.317 | 3.09 | - | VBGF parameters from Coyne (2000; Tab. 4, p. 59). Unexploited; stranded head-start turtles; $W_\infty$ from Tab 1 (32b). |
| | h | | G. Mexico, USA | 722 | U | 74.3 | SCL | 40.1 | 1.42 | - | - | 0.280 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 12-13, p. 28-30). Unexploited; 0-71 cm. $W_\infty$ from Tab 1 (32b). K=ave. $\Phi'$; same species. |
| | i | | NMFS Statistical Zone, USA | 256 | U | 68.5 | SCL | 31.9 | 1.96 | - | - | 0.329 | $L_\infty$ from single L/F histogram from Coyne (2000; Fig. 21, p. 45). Unexploited; stranded sea turtles; 15-61 cm. $W_\infty$ from Tab 1 (32b). K=ave. $\Phi'$; same species. |
| | j | | N G. Mexico, Atlantic coast, USA | 96 | U | 70.7 | SCL | 34.9 | - | 0.200 | 3.00 | - | Fitted VBGF from Schmid and Woodhead (1998; Eq. 2, p. 96). To= -0.32; Unexploited; 22-67 cm; mark-recapture. $W_\infty$ from Tab 1 (32b). |
| | k | | N. G. Mexico, USA | 58 | U | 71.1 | SCL | 35.4 | - | 0.210 | 3.03 | - | Fitted VBGF from Schmid and Woodhead (1998; Eq. 1, p. 96); $t_0$=-0.31; unexploited; 22-68 cm; tag-recapture. $W_\infty$ from Tab 1 (32b). |
| | l | | Sambine Pass, G. Meixco, USA | 189 | U | 56.2 | SCL | 18.2 | 2.12 | - | - | 0.488 | $L_\infty$ from single L/F histogram from Coyne (2000; Fig. 21, p. 45). Unexploited; 20-51 cm. $W_\infty$ from Tab 1 (32b). K=ave. $\Phi'$; same species. |
| | m | | Apalachee Bay, USA | 102 | U | 62.7 | SCL | 24.8 | 2.07 | - | - | 0.392 | $L_\infty$ from single L/F histogram from Schmid (2000; Fig. 1-3, p. 10). Unexploited; 20-56 cm. $W_\infty$ from Tab 1 (32b). K=ave. $\Phi'$; same species. |
| | n | | W Atlantic | 1028 | U | 77.6 | SCL | 45.4 | 1.93 | - | - | 0.256 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 11-13, p. 26-30). Unexploited; 0-71 cm. $W_\infty$ from Tab 1 (32b). K=ave. $\Phi'$; same species. |
| | o | | Withlacoochee and Crystal Rivers, USA | 76 | U | 56.7 | SCL | 18.7 | 2.09 | - | - | 0.479 | $L_\infty$ from single L/F histogram from Schmid (2000; Fig. 1-3, p. 10). Unexploited; 25-50 cm. $W_\infty$ from Tab 1 (32b). K=ave. $\Phi'$; same species. |
| 25 | a | *Lepidochelys olivacea* | G. Mannar, India | 99 | U | 73.8 | CCL | 49.2 | 0.758 | - | - | 0.177 | $L_\infty$ from single L/F histogram from Bhupathy and Saravanan (2006; Fig. 2, p. 140). Exploited; 46-72 cm; narrow range, may not be a good representative of the population. $W_\infty$ from Tab 1 (33c). $L_\infty$ assummed as SCL; K=ave. $\Phi'$; Cheloniidae. |
| | b | | N. Territory, Australia | 85 | F | 77.0 | CCL | 50.6 | 2.87 | - | - | 0.163 | $L_\infty$ from single L/F histogram from Whiting *et al.* (2007; Fig. 4, p. 205). Unexploited; 64-76 cm. $W_\infty$ from Tab 1 (33a). $L_\infty$ assummed as SCL; K=ave. $\Phi'$; Cheloniidae. |

**Table A2**. Continued.

| Spec. No. | Stock No. | Species | Locality | N | Sex | $L_\infty$ cm | Type | $W_\infty$ kg | Z/K (or Z) | K years$^{-1}$ | Φ' | K from Φ' | Method/Comments/Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 25 | c | *Lepidochelys olivacea* | Queensland, Australia | 31 | U | 84.3 | CCL | 69.8 | 1.99 | - | - | 0.136 | $L_\infty$ from single L/F histogram from Robins (2007; Fig. 2, p. 163). Exploited; 20-71 cm. $W_\infty$ from Tab 1 (33b). $L_\infty$ assummed as SCL; K=ave. Φ'; Cheloniidae. |
| 26 | a | *Natator depressus* | Curtis Island, Australia | 48 | F | 100.5 | CCL | 107 | 2.68 | - | - | 0.095 | $L_\infty$ from single L/F histogram from Limpus *et al.* (2006 ; Fig. 2, p. 10). Unexploited; nesting females; 89-99 c; Woongarra coast not included. $W_\infty$ from Tab 1 (34a). $L_\infty$ assummed as SCL; K=ave. Φ'; Cheloniidae. |
|  | b |  | Queensland, Australia | 76 | U | 114.2 | CCL | 156 | 2.12 | - | - | 0.074 | $L_\infty$ from single L/F histogram from Robins (2007; Fig. 2, p. 163). Exploited; 20 to 101 cm. $W_\infty$ from Tab 1 (34a). $L_\infty$ assummed as SCL; K=ave. Φ'; Cheloniidae. |
| 27 | a | *Dermochelys coriacea* (Testudines, Dermochelydae) | G. Mexico, USA | 41 | U | 164.1 | SCL | 521 | 1.17 | - | - | 0.057 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 18-19, p. 40-42). Unexploited; 100-160 cm. $W_\infty$ from Tab 1 (35d). K=Φ'; same species. |
|  | b |  | Nova Scotia, Canada | 120 | U | 162.2 | SCL | 420 | 1.94 | - | - | 0.033 | $L_\infty$ from single L/F histogram from James *et al.* (2007; Fig. 1, p. 248). Unexploited; 125-166 cm. $W_\infty$ from Tab 1 (35d). K=Φ'; same species. |
|  | c |  | off coast, France | 82 | U | 150.1 | SCL | 338 | 1.57 | - | - | 0.039 | $L_\infty$ from single L/F histogram from James *et al.* (2007; Fig. 1, p. 248). Unexploited; 100-156 cm. $W_\infty$ from Tab 1 (35d). K=Φ'; same species. |
|  | d |  | Vancouver, Canada | 101 | U | 155.0 | SCL | 370 | - | 0.270 | 3.81 | - | VBGF parameters from Jones *et al.* (2008; Tab. 1). To= -0.12; unexploited; maintained in captivity from hatchlings to > 2-years; $W_\infty$ from Tab 1 (35d). |
|  | e |  | W. Atlantic | 243 | U | 105.0 | SCL | 124 | - | - | - | 0.140 | $L_\infty$ from single L/F histogram from Teas (1993; Tab. 17-19, p. 38-42). Unexploited; 10-101 cm. $W_\infty$ from Tab 1 (35d). K=Φ'; same species. |

**Table A3**. Maturity data assembled for sea snakes and sea turtles used to obtain Figure 4.

| Spec. No. | Stock No. | Species | Locality | Sex | $L_m$ (cm) | Comments/Remarks |
|---|---|---|---|---|---|---|
| 1 | a | *Acalyptophis peronii*<br>(Squamata, Hydrophiidae) | northern Australia | unsexed | 71.6 | $L_m$ max 114 cm from Milton (2001). |
| | b | | northern Australia | M | 89 | $L_m$ range 70.3 - 113.9 cm from Fry *et al.* (2001). |
| | c | | northern Australia | F | 71.6 | $L_m$ range 70.2 - 110.8 cm from Fry *et al.* (2001). |
| 2 | a | *Aipysurus apraefrontalis* | northern Australia | M | - | $L_m$ min 92 cm from Fry *et al.* (2001). |
| 3 | a | *Aipysurus duboisii* | northern Australia | unsexed | 91 | $L_m$ max 117 cm from Milton (2001). |
| | b | | northern Australia | F | 91 | $L_m$ range 91 - 116.2 cm from Fry *et al.* (2001). |
| | c | | northern Australia | M | - | $L_m$ range 57 - 116.5 cm from Fry *et al.* (2001). |
| 4 | a | *Aipysurus eydouxii* | northern Australia | unsexed | 47.2 | $L_m$ max 85 cm from Milton (2001). |
| | b | | northern Australia | M | 64 | $L_m$ range 54.7 - 78 cm from Fry *et al.* (2001). |
| | c | | northern Australia | F | 47.2 | $L_m$ range 39.2 - 85 cm from Fry *et al.* (2001). |
| 5 | a | *Aipysurus laevis* | northern Australia | unsexed | 103 | $L_m$ max 130 cm from Milton (2001). |
| | b | | northern Australia | M | 102 | $L_m$ range 64 - 106 cm from Fry *et al.* (2001). |
| | c | | northern Australia | F | 103 | $L_m$ range 71.2 - 130 cm from Fry *et al.* (2001). |
| 6 | a | *Astrotia stokesii* | northern Australia | M | 72 | $L_m$ range 59.5 - 122 cm from Fry *et al.* (2001). |
| | b | | northern Australia | F | 81.7 | $L_m$ range 71.4 - 138 cm from Fry *et al.* (2001). |
| | c | | northern Australia | unsexed | 81.7 | $L_m$ max 138 cm from Milton (2001). |
| 7 | a | *Disteira kingii* | northern Australia | unsexed | 82.3 | $L_m$ max 165 cm from Milton (2001). |
| | b | | northern Australia | M | 145 | $L_m$ range 66.1 - 162 cm from Fry *et al.* (2001). |
| | c | | northern Australia | F | 82.3 | $L_m$ range 78.9 - 157.2 cm from Fry *et al.* (2001). |
| 8 | a | *Disteira major* | northern Australia | unsexed | 71 | $L_m$ max 165 cm from Milton (2001). |
| | b | | northern Australia | M | 84 | $L_m$ range 53 - 163.5 cm from Fry *et al.* (2001). |
| | c | | northern Australia | F | 71 | $L_m$ range 61.5 - 143.1 cm from Fry *et al.* (2001). |
| 9 | a | *Emydocephalus annulatus* | northern Australia | M | - | $L_m$ min 880 cm from Fry *et al.* (2001) |
| 10 | a | *Enhydrina schistosa* | Sourabaya, Java, Indonesia | M | 70 | Length at the beginning of maturity from Bergman (1943). |
| | b | | Sourabaya, Java, Indonesia | F | 70 | Length at the beginning of maturity from Bergman (1943). |
| | c | | northern Australia | unsexed | 79 | $L_m$ max 102.4 cm from Milton (2001). |
| | d | | northern Australia | F | 79 | $L_m$ range 47.1 - 101.5 cm from Fry *et al.* (2001). |
| | e | | northern Australia | M | - | $L_m$ range 56 - 88.1 cm from Fry *et al.* (2001). |
| 11 | a | *Hydrophis brookii* | Sourabaya, Java, Indonesia | M | 65 | Length at the beginning of maturity from Bergman (1943). |
| | b | | Sourabaya, Java, Indonesia | F | 65 | Length at the beginning of maturity from Bergman (1943). |
| 12 | a | *Hydrophis caerulescens* | northern Australia | F | 84 | $L_m$ range 71 - 84 cm from Fry *et al.* (2001). |
| | b | | northern Australia | M | - | $L_m$ range 76 - 94.7 cm from Fry *et al.* (2001). |
| 13 | a | *Hydrophis cyanocinctus* | Sourabaya, Java, Indonesia | M | 70 | Length at the beginning of maturity from Bergman (1943). |
| | b | | Sourabaya, Java, Indonesia | F | 70 | Length at the beginning of maturity from Bergman (1943). |

**Table A3**. Continued.

| Spec. No. | Stock No. | Species | Locality | Sex | *Lm* (cm) | Comments/Remarks |
|---|---|---|---|---|---|---|
| 14 | a | *Hydrophis czeblukovi* | northern Australia | F | 98 | $L_m$ min 98 cm from Fry *et al.* (2001). |
| 15 | a | *Hydrophis elegans* | northern Australia | unsexed | 118 | $L_m$ max 227 cm from Milton (2001). |
|  | b |  | northern Australia | M | 89 | $L_m$ range 51.2 - 172 cm from Fry *et al.* (2001). |
|  | c |  | northern Australia | F | 118 | $L_m$ range 90.4 - 22.7 cm from Fry *et al.* (2001). |
| 16 | a | *Hydrophis fasciatus* | Sourabaya, Java, Indonesia | F | 65 | Length at the beginning of maturity from Bergman (1943). |
|  | b |  | Sourabaya, Java, Indonesia | M | 60 | Length at the beginning of maturity from Bergman (1943). |
| 17 | a | *Hydrophis inornatus* | northern Australia | F | 92 | $L_m$ min 92 cm from Fry *et al.* (2001). |
| 18 | b |  | northern Australia | unsexed | 63.5 | $L_m$ max 91.2 cm from Milton (2001). |
|  | c |  | northern Australia | M | 78 | $L_m$ range 76 - 91.2 cm from Fry *et al.* (2001). |
|  | d |  | northern Australia | F | 63.5 | $L_m$ range 35.1 - 82 cm from Fry *et al.* (2001). |
| 19 | a | *Hydrophis ornatus* | northern Australia | unsexed | 80 | $L_m$ max 163 cm from Milton (2001). |
|  | b |  | northern Australia | M | 85 | $L_m$ range 81.2 - 126 cm from Fry *et al.* (2001). |
|  | c |  | northern Australia | F | 80 | $L_m$ range 70 - 157.4 cm from Fry *et al.* (2001). |
| 20 | a | *Hydrophis pacificus* | northern Australia | unsexed | 135 | $L_m$ max 165 cm from Milton (2001). |
|  | b |  | northern Australia | M | 141 | $L_m$ min 141 cm from Fry *et al.* (2001). |
|  | c |  | northern Australia | F | - | $L_m$ range 135 - 165 cm from Fry *et al.* (2001). |
| 21 | a | *Lapemis hardwickii* | Sourabaya, Java, Indonesia | M | 44 | Length at the beginning of maturity from Bergman (1943). |
|  | b |  | Sourabaya, Java, Indonesia | F | 44 | Length at the beginning of maturity from Bergman (1943). |
|  | c |  | northern Australia | unsexed | 67.7 | $L_m$ max 125 cm from Milton (2001). |
|  | d |  | northern Australia | M | 54 | $L_m$ range 44.2 - 118 cm from Fry *et al.* (2001). |
|  | e |  | northern Australia | F | 67.7 | $L_m$ range 33 - 113 cm from Fry *et al.* (2001). |
| 22 | a | *Laticauda semifasciata* | near Orchid Island, Taiwan | M | 70 | Minimun SVL at sexual maturity; Ave. water temperature of Kuroshio current 26°C (21-29°C). $L_m$ range 70-80 cm from Tu *et al.* (1990). |
|  | b |  | near Orchid Island, Taiwan | F | 80 | Tu *et al.* (1990) |
| 23 | a | *Thalassophis anomalus* | Sourabaya, Java, Indonesia | M | 42.5 | Length at the beginning of maturity from Bergman (1943). |
|  | b |  | Sourabaya, Java, Indonesia | F | 42.5 | Length at the beginning of maturity from Bergman (1943). |
| 24 | a | *Caretta caretta* (Testudines, Cheloniidae) | Merritt Island, Florida, USA | unsexed | - | Estimated VBGF range of age at maturity; $t_m$= 12-30. $L_m$ range 74-92 cm from Frazer and Ehrhart (1985). |
| 25 | a | *Chelonia mydas* | Merritt Island, Florida, USA | unsexed | - | Estimated VBGF range of age at maturity; $t_m$= 18-27. $L_m$ range 88-99 cm from Frazer and Ehrhart (1985). |
| 26 | a | *Lepidochelys kempii* | Gulf of Mexico, USA | unsexed | 60 | Stranded head-starts; $t_m$= 10 from Coyne (2000). |
|  | b |  | Florida, USA | unsexed | 62.5 | Recaptured wild and head-started turtles; $t_m$= 9 from Coyne (2000). |

# GROWTH OF LEATHERBACK SEA TURTLES (*DERMOCHELYS CORIACEA*) IN CAPTIVITY, WITH INFERENCES ON GROWTH IN THE WILD[1]

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## ABSTRACT

Leatherback turtles (*Dermochelys coriacea*) are critically endangered with current population trends in the Pacific indicating that they are nearing extinction. Their recovery will depend on coupling strong conservation measures with knowledge of their life history, particularly growth. Until now, however, there was considerable uncertainty on the growth on both juvenile and adults in the wild. The research reported here marks the first time that several leatherback juveniles have been maintained for over two years in captivity, and we discuss our experiences raising these leatherbacks from hatchlings (50 g) to juveniles (> 40 kg) for studies on their early growth. We derived a length-weight relationship of the form W (kg) = 0.000264 · SCL (cm)^2.806, which fitted both ours, and 10 turtles sampled from the wild. Also, a von Bertalanffy growth curve was derived whose parameters ($SCL_\infty$ = 155 cm; K = 0.266 $year^{-1}$ and $t_0$ = -0.12 year) predicts, for a length at first maturity of 135 cm, an age of 7 years, in agreement with earlier studies of the hard parts of leatherbacks. These results are in agreement with the known biology of leatherbacks; some of their implications for the study of leatherback biology are discussed.

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## INTRODUCTION

All seven species of marine turtle are threatened, with several species listed as endangered or critically endangered (IUCN, 2007). Detailed knowledge of their life-history, notably the time they spend in various feeding grounds and their age at first maturity is essential for conservation (Seminoff *et al.*, 2002; Chaloupka & Musick 1997). This requires a knowledge of growth rate at all stages (or of size-at-age), which is best summarized by the parameters of a growth equation, e.g., the von Bertalanffy Growth Function (VBGF) for length and weight (von Bertalanffy, 1938).

Once a 'standard growth curve' has been established, it is then straightforward to evaluate growth in different populations, which should aid in our understanding of the variability in geographically separated foraging grounds and allow quantitative and qualitative comparisons of the foraging areas, based on the ability of a habitat to meet the ecological requirements of marine turtles (Bjorndal & Jackson, 2003; Bjorndal *et al.*, 2000; Bjorndal & Bolten, 1988).

Most studies of marine turtle growth have focused on the cheloniid species (see Chaloupka & Musick, 1997, Palomares *et al.*, 2008) while relatively few have focused on leatherbacks. This is not surprising when considering the near-exclusive oceanic lifestyle of leatherbacks, of which the female go on land only for nesting, and the near impossibility of maintaining them in captivity (Jones *et al.*, 2000). Yet, leatherbacks are listed as critically endangered (IUCN, 2007) and may be nearing extinction in the Pacific (Spotila *et al.*, 2000). Within two decades the number of adult females in the Pacific declined from ~ 91,000 to under 3,000 (Spotila *et al.*, 2000; 1996). We need to have information on the basic biology of leatherbacks, including demographics and life-history patterns, if we are to stop, and hopefully reverse, their decline.

Leatherbacks are the largest (Buskirk & Crowder, 1994) of the marine turtles, but there are few reports on adult growth rates (Price *et al.*, 2004; Zug & Parham, 1996). The growth of juvenile leatherbacks in the wild, moreover, is completely unknown, due to their distribution being largely unknown, thus precluding marking-recapture studies of their growth.

Marking-recapture studies with marine turtles other than leatherbacks suggest they reach sexual maturity at an age of 20-30 years (Chaloupka & Musick, 1997), but recent evidence based on the study of hard parts in wild leatherbacks suggests an early attainment of minimum nesting sizes, i.e., as early as 3-6 years (Rhodin, 1985), or 6 years (Zug & Parham, 1996).

Herein, we describe how we derived the parameters of the VBGF for length and weight growth in leatherback, by combining and harmonizing the results of several studies, notably our own growth experiment on captive leatherbacks, i.e., 20 hatchlings raised from emergence to > 2 years of age in the laboratory. We then suggest, in the light of the coherence of the results obtained, that the growth curves presented below can serve as standard growth curves for leatherback turtles.

## MATERIALS AND METHODS

### *Captive rearing experiments*

Leatherback turtles were obtained on Canada CITES import permit CA05CWIM0039 and British Virgin Islands CITES Export certificate CFD062005. These animals are housed and maintained for research purposes and we meet all the ethical animal care standards as put forth by the Canadian Council for Animal Care (CCAC) and the UBC Animal Care Committee (UBC Animal Care Protocol: A04-0323).

Twenty hatchlings (emergence July 2nd, 2005) were transported from Tortola, BVI to the Animal Care Center, Department of Zoology, University of British Columbia. Animals were reared at the South Campus Animal Care facility using protocols developed by Jones *et al.* (2000). The three main obstacles to overcome in rearing leatherbacks are (i) their oceanic-pelagic nature (no recognition of barriers), (ii) designing a food matching their gelatinous food in the wild, and (iii) water quality.

As leatherbacks are oceanic-pelagic animals, which do not recognize vertical (tank walls) and horizontal barriers (tank bottom), the animals were tethered to PVC™ pipes secured across the tops of the tanks. Animals < 10 kg were attached to the tether using Velcro™ and cyanoacrylate cement attaching the tether to the posterior portion of their carapace, thus confining them to a section of the tank. Each hatchling could swim or dive in any direction, but was unable to contact other turtles or the tank's bottom and walls. Upon reaching ≥ 10 kg the juveniles were secured to the tether with a harness made of Tygon™ tubing. The harness circled each shoulder like a backpack and then looped around the caudal peduncle of the animal. Harnessing the leatherbacks is necessary as they swim continuously and, failing to recognize physical barriers, would abrade their skin against such barriers, which would lead to infections and usually death (Jones *et al.*, 2000).

The turtles were fed 3 to 5 times daily to satiation during the first 2-months of age and 3 times daily to satiation when > 2 months of age on a squid gelatin diet. The diet consists of squid (Pacific Ocean squid; mantle and tentacles only), vitamins (Reptavite™) and calcium (Rep-Cal™), blended with flavorless gelatin and hot water. As the wild diet of leatherbacks consists solely of gelatinous zooplankton (i.e., jellyfish; see Pauly *et al.* 2008), it is necessary for the food to have the proper texture and consistency.

The food was weighed (Ek-1200 A; Stites Scale Inc., 3424 Beekman Street, Cincinnati, OH 45223) prior to feeding and notes were made as to individual food mass intake per day. The food had a water content of 90 % water, and an energy content of 20.16 ± 0.39 kJg$^{-1}$ (dry weight). Random food samples were dried in a desiccating oven at 60°C for 24 to 72 hours to determine the dry to wet weight ratio. The dried homogenized samples were then sent to the Southwest Fisheries Science Center of NOAA (La Jolla, California, USA) for analysis with a bomb calorimeter (Parr Instrument Co.).

The turtles were maintained in large oval tanks (5 m long x 1.5 m wide x 0.3 m deep) containing ~ 2,500 l of re-circulated/filtered salt water. Water temperature was maintained at 24 ± 1 °C. Four fluorescent fixtures (40 W UVA/B; Repti-Glow 8) suspended 0.5 m above each pool provided full spectrum radiation on a 12/12 hour cycle; also, each tank received ambient light. Water quality was maintained to the following levels pH = 8.0 to 8.3; salinity = 28-33, and ammonia < 0.1 mg$^{-1}$. Water quality for each pool was maintained by four systems: a biological filter, a sand filter (Triton II™), an ultraviolet filter (Aqua Ultraviolet™ 114 W UV water sterilizer) and a protein skimmer.

The turtles were weighed and measured on emergence, at 3 and 7 days of age, then weekly. Straight carapace length (SCL), the distance from the center of the nuchal notch to the caudal peduncle (posterior of the carapace), was used for all length measurements, and performed with a digital caliper to the nearest 0.1 mm. The turtles were weighted using an Ek-1200 A scale (Stites Scale Inc., 3424 Beekman Street, Cincinnati, OH 45223) from hatching to weights of 1.2 kg (± 0.1g), and an ADAM CPW-60 scale (Dynamic Scales, 1466 South 8th Street, Terre Haute, IN 47802) for weights ≥ 1.2 kg (± 0.02 kg).

### *Length-weight relationships and growth curves*

We fitted the available length-weight data pairs (Table 1 and 2) with a length weight relationship of the form:

$$W = a \cdot L^b \qquad \text{... 1)}$$

where W is the weight in kg, L the SCL in cm, a is a multiplicative parameter of dimension L·W$^{-1}$, and b is an exponent usually taking values near 3 (which then indicates isometric growth, and allows interpretation of 'a' as a condition factor; Pauly, 1984).

Equation (1) was fitted by first transforming the data of Table 1 into $\log_{10}W_i$ - $\log_{10}L_i$ pairs, and fitting these by a linear regression of the form:

$$\log_{10}W_i = \alpha + b \cdot \log_{10}L_i \qquad \text{... 2)}$$

where antilog α = a, and all other parameters are as defined previously.

The VBGF for length has the form:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad \text{... 3)}$$

where $L_t$ is the predicted length at age t, $L_\infty$ is the mean the adults of the population in question would reach if they were to grow for a very long time (indefinitely, in fact), K is a growth parameter (not a growth rate) of dimension time$^{-1}$, and $t_0$ is the age of the turtles at length=0.

It is a property of the VBGF that its first derivative (dl/dt) declines linearly with length, reaching zero at $L_\infty$. Hence, its parameter K can be estimated by plotting observed growth increments ($\Delta l/\Delta t$) against the mid-lengths of the increments (Pauly, 1984; Gulland & Holt, 1959), or

$$Y_i = a - K\overline{X_i} \qquad \text{... 4)}$$

where $Y_i = L_{i2}-L_{i1}/t_2-t_{i1}$, $\overline{X_i} = L_{i1}+L_{i2}/2$, and $L_{i1}$ and $L_{i2}$ are length measurements taken at the start and end of an arbitrary time interval $t_{i1}$ to $t_{i2}$. Also, we have $L_\infty = a/K$. This method leads to robust estimate of K, provided that the intervals $t_{i1}$ to $t_{i2}$ are relatively short, as in this case (Gulland & Holt, 1959). Its main advantage is that it provides for visualization of the data, and thus to identify outliers or incompatible data sets (Pauly, 1984). The method can also be modified to allow for estimation of K even when growth increments are available only for juveniles. In such cases, a forcing value of $L_\infty$ is used, and $K = \overline{Y}_i/(L_\infty - \overline{X}_i)$ (Pauly, 1984). We used 155 cm SCL (mean length of nesting females) as forcing value of $L_\infty$, based on studies in both the Atlantic (Boulon *et al.*, 1996) and the Pacific (Price *et al.*, 2004).

Another approach to fitting the VBGF is iterative, non-linear fitting (e.g., Fabens, 1965). Here, this was performed using the Sigma Plot software, with $L_\infty$=155 cm as constraint, given that the narrow range of the length-at age data fitted (Table 1) would not have otherwise lead to convergence.

The VBGF for weight has the form:

$$W_t = W_\infty(1 - e^{-K(t-t_0)})^b \qquad \text{... 5)}$$

where $W_\infty$ is the weight corresponding to $L_\infty$, e.g., as estimated by Equation (1), b the exponent of that same length-weight relationship, and all other parameters are defined as for the VBFG for length (Equation 3).

## RESULTS AND DISCUSSION

The hatchlings averaged 0.046 ± 0.001 kg body mass and 6.32 ± 0.13 cm SCL (straight carapace length) upon emergence. All hatchlings began feeding on the formulated squid gelatin by 3-5 days post emergence. Four turtles survived 18 months post emergence, with only 2 surviving more than 2 years. The largest animal was 42.65 kg and 72.0 cm SCL at 26 months old (age at death). Due to space constraints, we give here only a subset of the length and weight measurements taken during the life span of all 20 hatchlings (Table 2). Despite the deaths, the feeding regime seemed adequate, as assessed by the fact that our captive animals matched the condition of wild leatherbacks (Figure 1). The

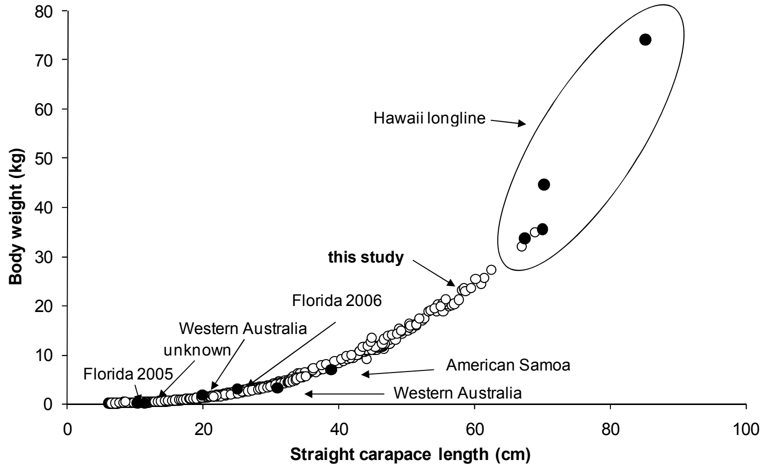

**Figure 1**. Plot of weight *vs*. length in 20 leatherbacks turtles maintained in captivity, from hatchlings to > 2-years (this study, Table 1) compared with weight *vs*. length from strandings and by-catch (Table 2). The overlap between the two data sets suggests that conditions for the captive turtles corresponded to those in the wild (c.f. with Figure 2).

relationship we obtained from the N = 101 log-transformed length and weight data pairs in Tables 1 and 3 ($r^2 = 0.998$) is:

$$W = 0.000264 \cdot L^{2.806} \quad \text{... 6)}$$

where W is the weight in kg and L the SCL in cm.

The length and weight data pairs from our study match those of leatherback taken from the wild (Figure 1), and hence equation (4) may be proposed as standard L-W relationship for leatherback turtles. On the other hand, the data in Figure 1, and Equation (4) suggest that the turtles raised by Deraniyagala (1939) and Bels *et al.* (1988) suffered from sub-optimal condition, notably inadequate nutrition (i.e., algae, beef heart, and French bread; see Table 2), resulting in elevated mortality (Table 2), emaciation (Figure 2), and reduced growth (see below).

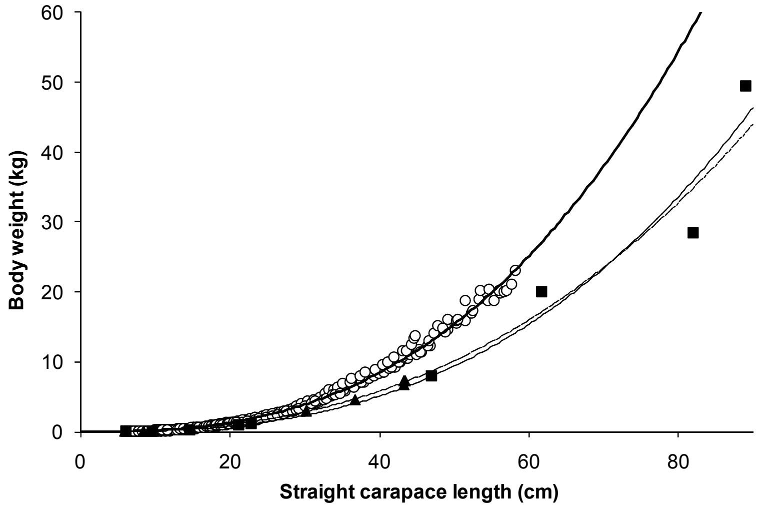

**Figure 2**. Length-weight relationships of leatherback turtles. Solid black line: relationship based on length and weight (open dots) of the turtles we maintained in captivity from hatchlings to > 2-years (this study, Table 1). Thin black line: relationship based on the turtles (black squares) reared by Bels *et al.* (1988). Dotted line: relationship based on the turtles (black triangles) reared by Deraniyagala (1939). The low weight at length of the turtles reared by Bels *et al.* and Deraniyagala suggest that they suffered from less than optimal conditions (c.f. with Figure 1).

Figure 3 contrasts the growth rates obtained in this study (Table 1) with those reported by Deraniyagala (1939) and Bels *et al.* (1988). Despite much variability, our turtles exhibited higher growth rates than theirs. Moreover, the juvenile growth rates we obtained appear compatible with the adult growth rates reported by Price *et al.* (2004). Figure 3 also demonstrates the compatibility of our results with those Zug and Parham (1996), who found that juvenile leatherback growth rates were 31.6 cm year$^{-1}$ for juveniles 8-37 cm SCL and 23.1 cm year$^{-1}$ for juveniles 37-65 cm SCL [data converted from curved-carapace lengths using the equation of Tucker & Frazer (1991)].

Our growth rate data, combined with a value of $L_\infty$ set at 155 cm allows estimation of a preliminary value of K = 0.232 from the slope of the plot in Figure 3. Fitted non-linearly, the same inputs yielded the VBGF for length:

$$L_t = 155(1-e^{-0.266(t+0.12)}) \quad \text{... 7)}$$

The resulting curve is shown in Figure 4, and contrasted with a curve based on the length-at-age data of Deraniyagala (1939) and Bels *et al.* (1988). As might be seen, our juvenile growth data suggest faster growth than theirs, as also shown in Figure 3.

Using 135 cm SCL as the minimum size at nesting, based on Boulon *et al.* (1996) for the Atlantic and Price *et al.* (2004) for the Pacific, Equation (8) suggests that it would take leatherbacks 7 years to reach sexual maturity, in agreement with the 6 years proposed by Zug & Parham (1996).

Combining Equation (6) with (7) leads, finally, to a VBGF for the growth in weight in leatherbacks, i.e.:

$$W_t = 370(1-e^{-0.266\,(t+0.12)})^{2.806} \quad \text{... 8)}$$

which can be used to predict mean weight at any age.

Major assumptions have been made in the experimental design of this study and for the results to have any validity they must be addressed. Firstly, the VBGF requires that growth be monotonic throughout postnatal development, as it displays no inflection points (Choulpka & Musick, 1997). Therefore, polyphasic growth data, or displaying an initial lag phase, would require another growth function, e.g., the Gompertz, logistic or others. However, the leatherback turtles we raised, and our longitudinal sampling (repeated sampling on the same individuals; Choulpka & Musick, 1997) resulted in growth data exhibiting neither polyphasic growth, nor a lag phase. Therefore, the use of the VBGF is justified in our case, and by extension, in leatherbacks as a whole. We also suspect this to be the case in other species of marine turtles, as well.

Captive growth does not necessarily reflect wild growth. However, our captive specimens exhibited the same length-weight relationships as wild juvenile leatherbacks (stranded or by-catch; Fig 1.), suggesting appropriate rearing conditions - at least compared with earlier captive growth studies. On the other hand, the problem of accelerated growth in captivity, seem to be limited to cheloniids (Swingle *et al.*, 1993;Wood & Wood, 1980), and may not occur in leatherbacks, whose chondro-osseous development characteristic suggests rapid growth (Rhodin *et al.*, 1996; Rhodin, 1985). Also, Zug & Parham (1996), whose growth data match ours almost perfectly (Figure 3), found rapid growth rates in wild leatherbacks (15 adults and 2 juveniles) and stated that the early captive growth pattern of leatherbacks closely matches the growth curves of wild individuals.

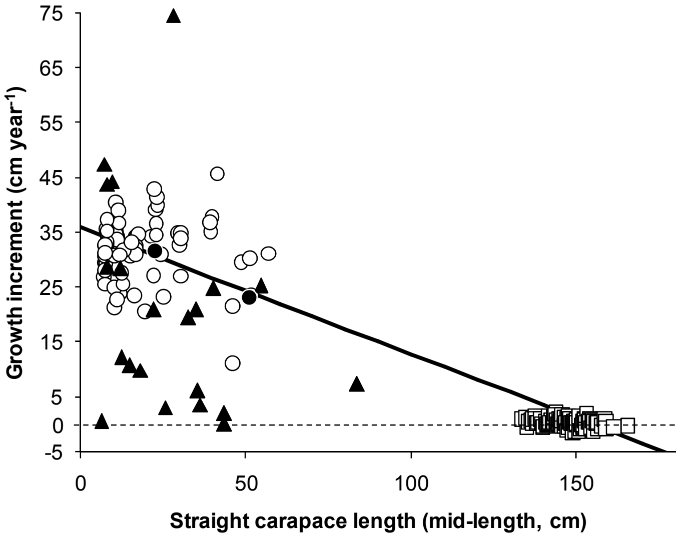

**Figure 3**. Plot of growth rates (Δl/Δt) against the corresponding mid-lengths of the growth increments in leatherback turtles, computed from Table 1 (open dots, our study), the studies of Deraniyagala (1939) and Bels *et al.* (1988) (black triangles), Zug & Parham (1996) (2 black dot) and adult growth rates from Price *et al.* (2004) (open squares). The solid line links the means of the values from our study (open dots) and $L_\infty$ = 155 cm (SCL); its slope allows a preliminary estimation of K = 0.232 year$^{-1}$. The data points from Deraniyagala (1939) and Bels *et al.* (1988) were omitted, as their turtles probably experienced suboptimal condition (c.f. Fig. 2, and see text).

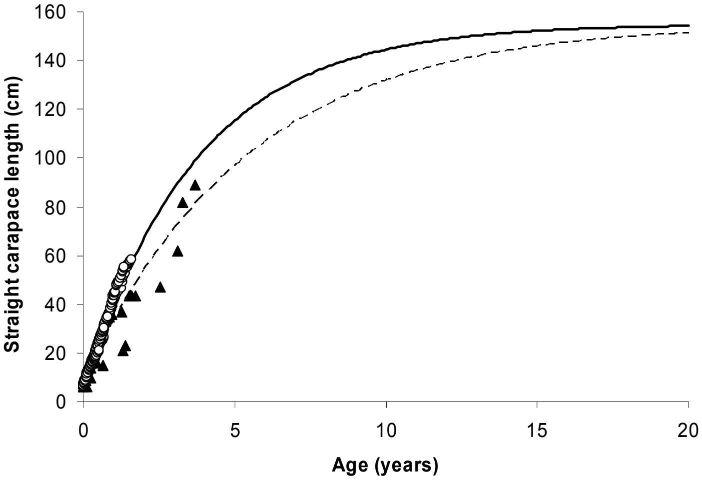

**Figure 4**. Von Bertalanffy Growth Functions for leatherback turtles: Solid line: VBGF with a fixed value of $L_\infty$ = 155 cm, K = 0.266 year$^{-1}$and $t_0$ = -0.12 year, based on length-at-age data in Table 1 (this study, open dots) fitted with SigmaPlot™ version 10. Dotted line: same $L_\infty$ and fitting method, with K = 0.185 year$^{-1}$ and $t_0$ = -0.03 year, derived from the length-at-age data in Table 3 (i.e., from studies of Deraniyagala, 1939 and Bels *et al.*, 1988, black triangles). The sub-optimal conditions suggested to have occurred in these studies affected the growth of the turtles.

Our findings confirm that leatherbacks mature a younger age (6-7 years, see above), but at a larger size than cheloniid turtles. For example, loggerheads take > 15 years to reach a sexually mature size of about 90 cm carapace length (Frazer & Ehrhart, 1985; Mendoca, 1981), whereas green turtles take > 20-30 years to reach sexual maturity at a carapace length of about 100 cm (Frazer & Ladner, 1986; Frazer & Ehrhart, 1985; Mendoca, 1981; Limpus & Walter, 1980). Similarly, green turtles with size of 30 cm spend nearly 20 years in juvenile habitats, before they acquire adult features (Seminoff *et al.*, 2002; Bjorndal & Bolten, 1988).

**Table 1.** Length and weight of 20 turtles raised in captivity from hatchling to ages of over 2 years, using the protocol and feed described in the text. N = 20 ≤ 12 months; 4 from 12 to 18 months; 2 from 18 months to > 24 months.

| Turtle ID | Age (days) | Weight (kg) | SCL (cm) | Turtle ID | Age (days) | Weight (kg) | SCL (cm) | Turtle ID | Age (days) | Weight (kg) | SCL (cm) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Dc 7 | 1 | 0.048 | 6.37 | Dc 13 | 31 | 0.115 | 8.61 | Dc 19 | 500 | 20.360 | 55.40 |
| Dc 7 | 31 | 0.139 | 9.25 | Dc 13 | 73 | 0.305 | 12.59 | Dc 20 | 1 | 0.047 | 6.55 |
| Dc 7 | 73 | 0.355 | 13.17 | Dc 13 | 157 | 1.260 | 20.04 | Dc 20 | 31 | 0.131 | 9.26 |
| Dc 8 | 1 | 0.046 | 6.10 | Dc 13 | 206 | 2.140 | 23.67 | Dc 20 | 73 | 0.349 | 13.49 |
| Dc 8 | 31 | 0.129 | 8.78 | Dc 14 | 1 | 0.048 | 6.32 | Dc 20 | 150 | 1.180 | 20.00 |
| Dc 8 | 73 | 0.342 | 13.29 | Dc 14 | 31 | 0.115 | 8.75 | Dc 20 | 206 | 2.480 | 26.33 |
| Dc 9 | 1 | 0.047 | 6.41 | Dc 14 | 101 | 0.489 | 14.99 | Dc 20 | 297 | 5.440 | 34.74 |
| Dc 9 | 31 | 0.123 | 8.82 | Dc 14 | 157 | 1.180 | 20.29 | Dc 21 | 1 | 0.045 | 6.29 |
| Dc 9 | 73 | 0.326 | 12.85 | Dc 14 | 206 | 2.160 | 24.93 | Dc 21 | 31 | 0.119 | 8.81 |
| Dc 9 | 157 | 1.280 | 20.69 | Dc 14 | 304 | 5.460 | 34.27 | Dc 21 | 87 | 0.300 | 12.05 |
| Dc 10 | 1 | 0.046 | 6.42 | Dc 14 | 402 | 11.000 | 44.14 | Dc 22 | 1 | 0.047 | 6.37 |
| Dc 10 | 31 | 0.124 | 9.03 | Dc 14 | 507 | 17.280 | 52.60 | Dc 22 | 31 | 0.127 | 9.11 |
| Dc 10 | 73 | 0.335 | 12.99 | Dc 14 | 611 | 25.600 | 61.50 | Dc 22 | 129 | 0.701 | 16.00 |
| Dc 10 | 157 | 1.220 | 20.20 | Dc 15 | 1 | 0.046 | 6.43 | Dc 23 | 1 | 0.047 | 6.24 |
| Dc 10 | 206 | 2.180 | 25.10 | Dc 15 | 31 | 0.133 | 9.05 | Dc 23 | 31 | 0.140 | 9.29 |
| Dc 10 | 304 | 5.420 | 34.46 | Dc 15 | 122 | 0.580 | 15.01 | Dc 23 | 122 | 0.754 | 17.15 |
| Dc 10 | 402 | 10.900 | 44.57 | Dc 16 | 1 | 0.045 | 6.13 | Dc 24 | 1 | 0.048 | 6.43 |
| Dc 10 | 500 | 12.060 | 47.50 | Dc 16 | 31 | 0.119 | 8.52 | Dc 24 | 31 | 0.117 | 8.72 |
| Dc 10 | 628 | 21.240 | 55.80 | Dc 16 | 73 | 0.360 | 13.16 | Dc 24 | 73 | 0.301 | 12.24 |
| Dc 11 | 1 | 0.046 | 6.04 | Dc 16 | 157 | 1.320 | 20.67 | Dc 24 | 150 | 1.020 | 19.21 |
| Dc 11 | 31 | 0.105 | 8.23 | Dc 16 | 248 | 3.420 | 28.38 | Dc 24 | 206 | 2.360 | 25.78 |
| Dc 11 | 73 | 0.264 | 11.90 | Dc 17 | 1 | 0.046 | 6.41 | Dc 24 | 332 | 5.580 | 35.13 |
| Dc 11 | 150 | 0.943 | 18.38 | Dc 17 | 31 | 0.144 | 9.32 | Dc 25 | 1 | 0.046 | 6.16 |
| Dc 11 | 206 | 2.000 | 23.65 | Dc 17 | 73 | 0.367 | 13.79 | Dc 25 | 31 | 0.117 | 8.83 |
| Dc 11 | 255 | 2.960 | 26.74 | Dc 18 | 1 | 0.047 | 6.38 | Dc 25 | 108 | 0.375 | 13.61 |
| Dc 12 | 1 | 0.046 | 6.44 | Dc 18 | 31 | 0.131 | 9.19 | Dc 26 | 1 | 0.046 | 6.33 |
| Dc 12 | 31 | 0.111 | 8.55 | Dc 18 | 66 | 0.263 | 11.57 | Dc 26 | 31 | 0.132 | 9.24 |
| Dc 12 | 73 | 0.303 | 12.59 | Dc 19 | 1 | 0.046 | 6.34 | Dc 26 | 108 | 0.496 | 15.03 |
| Dc 12 | 150 | 1.146 | 19.71 | Dc 19 | 31 | 0.135 | 9.20 | Dc 27 | 1 | 0.045 | 6.35 |
| Dc 12 | 206 | 2.460 | 25.73 | Dc 19 | 73 | 0.346 | 13.06 | Dc 27 | 31 | 0.125 | 8.91 |
| Dc 12 | 304 | 5.620 | 34.47 | Dc 19 | 157 | 1.280 | 20.39 | Dc 27 | 101 | 0.558 | 14.85 |
| Dc 12 | 402 | 10.420 | 43.87 | Dc 19 | 206 | 2.400 | 25.73 | Dc 27 | 150 | 0.900 | 17.98 |
| Dc 12 | 479 | 13.040 | 48.40 | Dc 19 | 304 | 6.360 | 35.03 | Dc 27 | 213 | 1.520 | 21.50 |
| Dc 13 | 1 | 0.046 | 6.19 | Dc 19 | 402 | 13.780 | 47.31 | - | - | - | - |

**Table 2.** Length and weight of 10 loggerhead turtles taken from the wild (stranded or as by-catch). Date, location and source are given for each turtle, except one, for which only the length and weight are known.

| Date | Location | Weight (kg) | SCL (cm) | Source |
|---|---|---|---|---|
| Aug-93 | American Samoa | 7.00 | 39.0 | MTN (1994; no 66, p. 3-5) |
| Sep-05 | Florida (2005) | 0.19 | 10.4 | J. Wyneken (*pers. comm.*) |
| Mar-06 | Florida (2006) | 3.10 | 25.0 | J. Wyneken (*pers. comm.*) |
| Apr-98 | Hawaii | 44.50 | 70.4 | NOAA (NMFS/PIFSC) |
| Apr-99 | Hawaii | 74.10 | 85.3 | NOAA (NMFS/PIFSC) |
| Apr-06 | Hawaii | 35.45 | 70.0 | NOAA (NMFS/PIFSC) |
| Jul-06 | Hawaii | 33.60 | 67.5 | NOAA (NMFS/PIFSC) |
| Jul-02 | W. Australia | 1.85 | 20.0 | MTN (2004; no. 104, p. 3-5) |
| 1983 | W. Australia | 3.30 | 31.0 | MTN (2004; no.104, p. 3-5) |
| Unknown | Unknown | 0.17 | 11.5 | M. Conti (*pers. comm.*) |

Turtles experience strong ontogenic habitat shifts. Thus, green turtles enter the oceanic-pelagic habitat as post-hatchling, and then turn into coastal-benthic feeders as juveniles (Bjorndal & Bolten, 1988), which probably induce a shift from an omnivorous to a herbivorous diet. These ontogenic habitat, diet and hence niche shifts may be the reason why the somatic growth of marine turtles often appears to be polyphasic (Hendrickson, 1980; Chaloupka & Musick, 1997). Leatherbacks, however, are oceanic-pelagic animals throughout their life-history (Bolten, 2003) and do not exhibit an ontogenetic diet shift; the diet consists solely of gelatinous zooplankton, throughout all life-history stages (Salmon *et al.*, 2004; Bjorndal, 1997). This, then, would justify the use of the VBGF.

Eckert (2002) used reports of visual sightings and incidental captures in north Atlantic to show that leatherbacks do not move above ~30° N and into water < 26 ℃ until they are over 100 cm in carapace length, corresponding given Equation (6) and (7), to an age of 3.8 years, and a weight of 108 kg, respectively. The latter value, used as an input for the leatherback thermoregulatory model of Bostrom & Jones (2007), suggest that these leatherbacks could maintain body temperatures 1.63 to 8.15 ℃ above ambient temperatures. This would allow them to move into colder waters where they can exploit different assemblages and perhaps greater abundance of gelatinous zooplankton, without their metabolism and growth being much reduced by the lower ambient temperatures. A review of reptilian growth by Avery (1994) showed that growth was not affected by cooler temperatures when the organisms were allowed to behaviorally thermoregulate. Although leatherback thermoregulation is endogenously driven, it is also a consequence of a large mass and locomotion (Bostrom & Jones, 2007). Thus, the benefit of higher body temperatures with regards to growth rates would not be lost to increased thermoregulatory costs.

**Table 3.** Length and weight at age of leatherback turtles raised from the hatchling stage to ages of over 1 year Deraniyagala (1939; initial N = 10; food: algae, beef hearts and French bread) and Bels *et al.* (1988; initial N = 14; food: mussels). Deraniyagala lost 90% his turtles in the first month, with 2 lasting 169 days, and 1 from day 169 to 662. Bels *et al.* lost 70% of their turtle within 2-months, with 1 lasting from day 183 to 1351.

| **Deraniyagala (1939)** | | | **Bels *et al.* (1988)** | | |
|---|---|---|---|---|---|
| **Age (days)** | **Weight (kg)** | **SCL (cm)** | **Age (days)** | **Weight (kg)** | **SCL (cm)** |
| 1 | 0.033 | 5.9 | 1 | 0.046 | 6.1 |
| 21 | 0.096 | 8.5 | 41 | 0.047 | 6.2 |
| 22 | -- | 7.3 | 85 | 0.075 | 9.6 |
| 32 | -- | 8.5 | 239 | 0.312 | 14.7 |
| 32 | -- | 8.9 | 478 | 0.950 | 21.2 |
| 46 | -- | 10.2 | 506 | 1.125 | 22.8 |
| 91 | -- | 13.7 | 726 | 3.720 | -- |
| 169 | -- | 16.0 | 847 | 4.500 | -- |
| 183 | -- | 25.4 | 928 | 8.020 | 47.0 |
| 195 | -- | 25.5 | 1140 | 20.000 | 61.7 |
| 203 | 2.438 | -- | 1200 | 28.500 | 82.0 |
| 218 | 3.005 | 30.2 | 1351 | 49.500 | 85.0 |
| 308 | -- | 35.0 | -- | -- | -- |
| 344 | -- | 35.6 | -- | -- | -- |
| 466 | 4.536 | 36.8 | -- | -- | -- |
| 562 | 6.804 | 43.3 | -- | -- | -- |
| 586 | 7.258 | 43.3 | -- | -- | -- |
| 624 | 7.265 | 43.5 | -- | -- | -- |
| 662 | -- | 42.0 | -- | -- | -- |

The decline in the Pacific leatherback population is daunting. The presumed cause is decades of intense egg harvest at most nesting beaches, exacerbated by widespread incidental by-catch from fisheries practices (Eckert & Sarti, 1997). Although the numbers of adults are higher in the Atlantic (~30,000), fishing practices continue to take their toll and the numbers from artisanal fisheries is unknown but probably severe (Peckham *et al.*, 2007). The good news is that with 7 years time to first nesting, leatherbacks still have a chance, as there is potential for a rapid rebound (at least compared with the slow-growing cheloniids) if fisheries by-catch can be reduced through moratoria and regulation.

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# LENGTH–WEIGHT RELATIONSHIPS AND ADDITIONAL GROWTH PARAMETERS FOR SEA TURTLES[1]

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## ABSTRACT

To facilitate field and other work on sea turtles, composite length-weight relationships, based on a wide range of sizes sampled by various authors, are presented for five species, viz. Kemp's ridleys (*Lepidochelys kempi*), olive ridleys (*Lepidochelys olivacea*), loggerheads (*Caretta caretta*), greens (*Chelonia mydas*), and hawkbills (*Eretmochelys imbricata*).

Also, 38 pairs of growth parameters of the von Bertalanffy growth function (VBGF; $K$; $L_\infty$ and $W_\infty$) are presented for four species, leaving only the growth of the olive ridley undocumented.

## INTRODUCTION

There are seven living species of sea turtles: flatback (*Natator depressus*), green sea turtle (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), Kemp's Ridley (*Lepidochelys kempi*), leatherback (*Dermochelys coriacea*), loggerhead (*Caretta caretta*), and olive ridley (*Lepidochelys olivacea*). Populations of all these species are threatened throughout the world because of overexploitation, disease, incidental capture by fishers, and destruction of critical nesting habitat (Lutcavage *et al.*, 1997; Mortimer *et al.*, 2000; Lewison *et al.*, 2004; Peckham *et al.*, 2008). Intensive, and sometimes sophisticated research has been conducted to quantify these impacts and inform management practices (e.g., Chaloupka & Balazs, 2007; Bailey *et al.*, 2008; e.g., Sims *et al.*, 2008). In the process, however, basic biological data are frequently overlooked. This applies particularly to morphometric relationships, whose validity is often taken for granted, although they tend to be based on too small a range of sizes to be of any use in building more elaborate models, e.g., turtle growth studies.

This contribution presents key morphometric data for 5 species of sea turtles, namely Kemp's ridleys (*L. kempi*), olive ridleys (*L. olivacea*), loggerheads (*C. caretta*), greens (*C. mydas*), and hawkbills (*E. imbricata*), and complements two other works in this volume, Jones *et al.* (2008) for leatherbacks and Palomares *et al.* (2008) for reptiles (including sea turtles).

## MATERIAL AND METHODS

The relationship between total length ($L$) and weight ($W$) for most animals is expressed by the equation:

$$W = a \bullet Lb \qquad \ldots 1)$$

whose parameters ($a$, $b$) are estimated by the antilog of the intercept, and the slope, respectively, of a regression of the $\log_{10} W$ against $\log_{10} L$. The value of $b$ is generally close to 3, implying 'isometry', i.e., the shape of the animal in question remaining the same as they get older and gain in size.

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**Table 1**. Empirical equations used to convert curved carapace length (CCL; cm) into straight carapace length (SCL; cm) measurements for individual species.

| Species | Equation | $R^2$ | Reference |
|---|---|---|---|
| *Lepidochelys kempi* | SCL = 0.957 * CCL - 0.696 | 0.99 | Plotkin (2007) |
| *Lepidochelys olivacea* | SCL = 0.818 * CCL + 9.244 | 0.91 | Whiting et al. (2007) |
| *Caretta caretta* | SCL = 0.948 * CCL – 1.442 | 0.97 | Teas (1993) |
| *Chelonia mydas* | SCL = 0.932 * CCL + 0.369 | 0.93 | Peckham et al. (2008) |
| *Eretmochelys imbricata* | SCL= 0.939 * CCL - 0.154 | n.a. | CITES (2002) |
| *Eretmochelys imbricata* | SCL = 0.935 * CCL + 0.449 | 0.99 | Limpus (1992) – for Australia |

Sea turtles can be measured in a number of ways, requiring standardisation before datasets can be compared. Straight carapace length (SCL) and curved carapace length (CCL) are the most commonly used measurements taken of sea turtles. As their name implies, CCL measurements are taken over the curve of the carapace whereas straight measurements are taken with a set of callipers. Although variations exist in how these measurements can be taken (e.g., notch to notch [NN] or notch to tip [NT]), authors most often do not detail the specific technique used in measuring individuals beyond curved or straight. For the purposes of this analysis, we assumed discrepancies to be minimal. Where necessary, data were converted to SCL using empirical equations listed in Table 1, based on linear regression of paired CCL and SCL data for the species in question.

To ensure that the parameters of length-weight relationships are estimated properly (Safran, 1992), length-weight data pairs from different studies were compiled to cover the widest possible range of sizes, and all developmental stages, i.e., juveniles, subadults, and adults (Table 2).

**Table 2**. Length weight relationships for 5 species of sea turtles; *a* and *b* are parameters in the equation of the type $W=a\,L^3$.

| Species | Location | *a* | *b* | $r^2$ | N | Size range (SCL; cm) | References |
|---|---|---|---|---|---|---|---|
| *Lepidochelys kempi* | Chesapeake, Florida, UK & France | 0.000247 | 2.834 | 0.958 | 145 | 19-67 | Carr & Caldwell (1956); Byles (1988); Campbell & Sulak (1997); Coles (1999); Witt *et al.* (2007) |
| *Caretta caretta* | Chesapeake, Florida, UK & France, Japan | 0.000282 | 2.823 | 0.966 | 431 | 12-105 | Byles (1988); Sato *et al.* (1995); Barichivich *et al.* (1997); Campbell & Sulak (1997); Coles (1999); Witt *et al.* (2007) |
| *Chelonia mydas* | Florida, Tortuguero, Ascension, Suriname, Baja, Solomon Islands | 0.000206 | 2.895 | 0.992 | 449 | 5-124 | Carr & Caldwell (1956); Pritchard *et al.* (1969); Barichivich *et al.* (1997); Campbell & Sulak (1997); (2000); Gilbert (2005); Seminoff *et al.* (2006); CCC (Unpublished); Krueger (unpublished); Seminoff & Jones (Seminoff & Jones) |
| *Lepidochelys olivacea* | Hawaii, Brazil, Suriname, Mozambique, Thailand, Australia | 0.000479 | 2.673 | 0.9955 | 46 | 4-74 | Pritchard *et al.* (1969); Hughes (1972); Chantrapornsyl (1992); Work & Balazs (2002); de Castilhos & Tiwari (2007); WWF-Australia (WWF-Australia) |
| *Eretmochelys imbricata* | Honduras, Cayman, Barbados, Suriname | 0.000278 | 2.736 | 0.988 | 112 | 22-99 | Pritchard *et al.* (1969); Beggs *et al.* (2007); Blumenthal *et al.* (2008); Dunbar *et al.* (2008) |

Although other growth curves exist to describe the growth of sea turtle (e.g. Bjorndal & Bolten, 1988; Chaloupka, 1998; Bjorndal *et al.*, 2000a; Chaloupka *et al.*, 2004), we have used the von Bertalanffy growth function (VBGF; von Bertalanffy, 1938) to ensure compatibility with the other growth parameters in this report. The VBGF for length has the form:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad \ldots 2)$$

where $L_t$ is the predicted length at age $t$, $L_\infty$ (also $L_{inf}$) is the mean the adults of the population in question would reach if they were to grow for a very long time (indefinitely, in fact), $K$ is a growth parameter (not a growth rate) of dimension time-1, and t0 is the age the turtles at length = 0.

Using the parameters $K$ (quantifying the curvature of the VBGF), and $L_\infty$ (or $W_\infty$, $W_{inf}$) one can then summarize and compare growth data by means of so called auximetric plots (Pauly, 1998).

The parameters $K$ and $L_\infty$ used for this analysis were taken from the published literature (see Table 3). Length-weight (L/W) relationships for each species, as described in Table 2, were then used to calculate $W_\infty$ (Table 3).

## RESULTS AND DISCUSSION

Table 1 summarizes available relationships between SCL and CCL, while Table 2 summarizes the L/W relationships and related data. The $r^2$ values for all L/W relationships were greater than 0.95. Estimates of parameter $b$ ranged from 2.673 for olive ridleys to 2.895 for green turtles. When split into individual 'populations' for each species $b$ spanned values between 2.495 and 3.134. This increased range in estimates reflected differences in 'population' sample sizes and length ranges. The L/W relationships for all 5 species, and the 'population' data used to derive them, are presented in Figure 1.

One potential application of such length-weight relationships is the computation of biomass estimates from length-frequency distributions. This is of great value when, for example, site and season-specific weights have not been collected due to logistical difficulties and/or lack of time required to record weight in the field. Although weight can be reliably estimated from length using equations such as those presented here, it should be noted that the exact relationship between length and weight may differ depending on the 'condition' of individual animals. Condition may reflect differences in food availability and population densities at individual sites (Bjorndal *et al.*, 2000a), and is likely to vary between seasons and years for a given population. In instances where the individuals of a population remain below the average curve, its individuals can be considered comparatively 'skinny'; conversely, when individuals lie above the curve, they can be considered 'stout'.

Notably, the compiled data presented here highlight the importance of obtaining 'true' estimates of population parameters through comprehensive sampling of a species size range. Relationships derived from morphometric data for a location-specific population may be biased by being representative of only a narrow size range. For example, because the majority of sea turtle programs operate on nesting beaches, length-weight data pairs are likely to be primarily, if not solely, collected from mature females. This can lead to erroneous population-level L/W relationships, as the juvenile-subadult phase is missing.

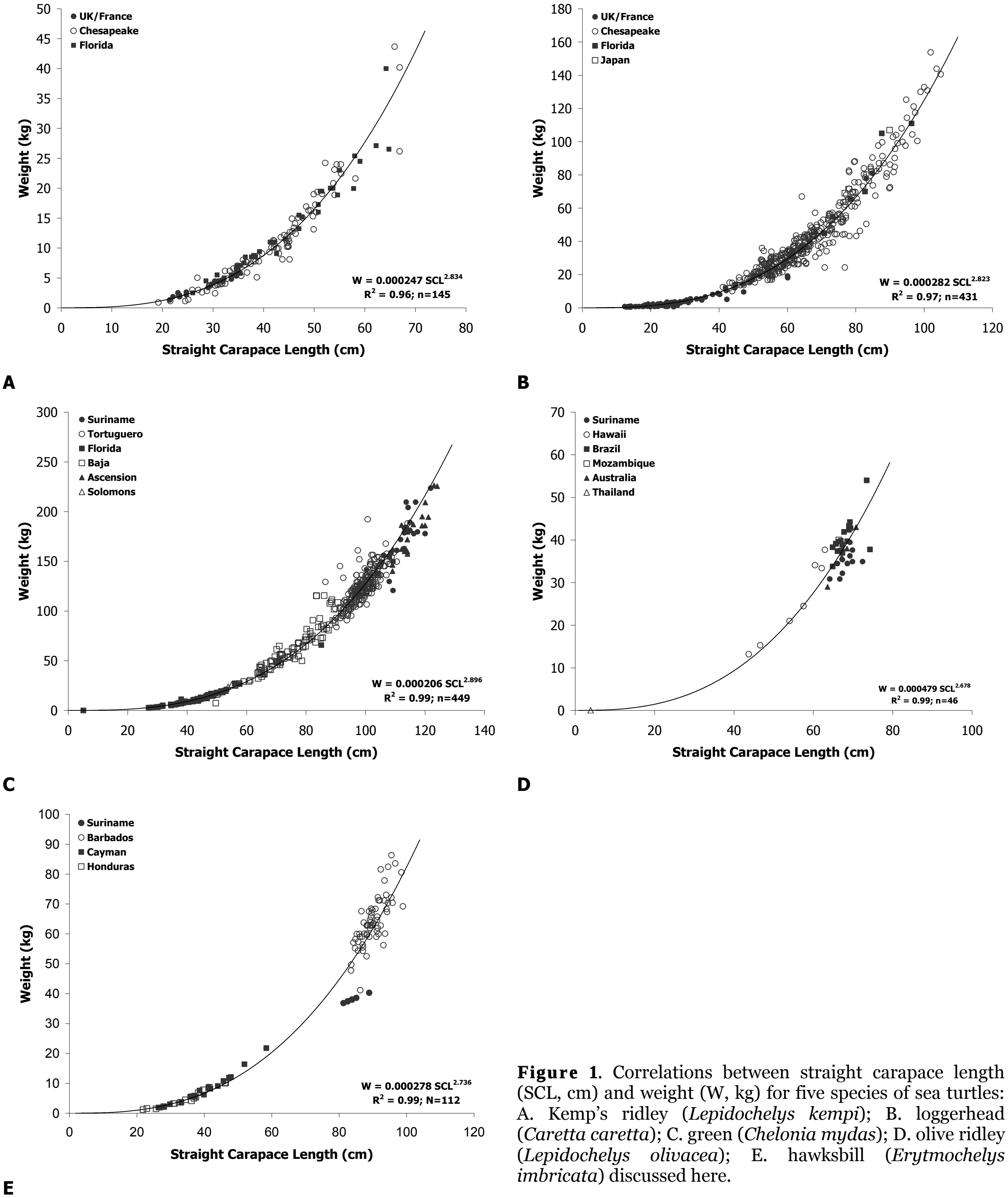

**Figure 1**. Correlations between straight carapace length (SCL, cm) and weight (W, kg) for five species of sea turtles: A. Kemp's ridley (*Lepidochelys kempi*); B. loggerhead (*Caretta caretta*); C. green (*Chelonia mydas*); D. olive ridley (*Lepidochelys olivacea*); E. hawksbill (*Erytmochelys imbricata*) discussed here.

Table A1 summarizes the growth parameters ($K$, $L_\infty$ and $W_\infty$), while the auximetric plot of Figure 2, which does not include outliers, shows that these growth parameters are mutually consistent.

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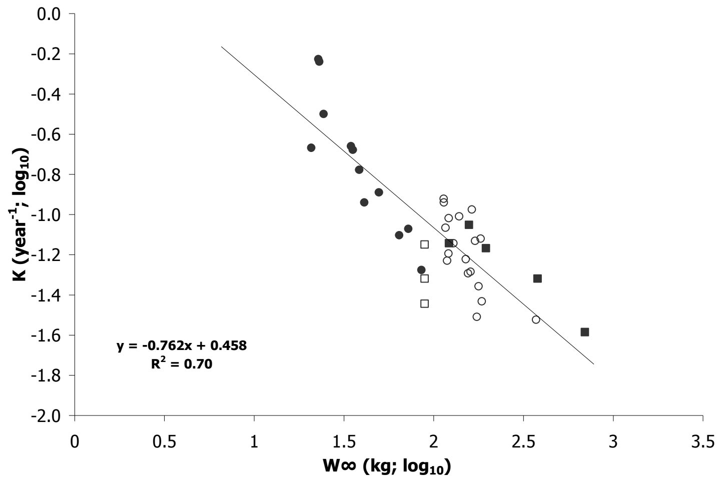

**Figure 2**. Auximetric plot of von Bertalanffy growth parameters for 38 data pairs of four species of sea turtles (see Table 3 for details). Dark circles represent data for *Lepidochelys kempi*, open circles *Caretta caretta*, dark squares *Chelonia mydas*, and open squares *Erytmochelys imbricata*

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**Table A1**. Additional growth parameter estimates for 4 species of sea turtles. Method: MR=Mark recapture; SC=Skeletochronology; LF=Length frequency. All data are from wild sea turtles except for data by Caillouet (1995) for *L. kempii*. Reported average lengths from http://www.nmfs.noaa.gov/pr/species/turtles /loggerhead.htm.

| **Species (reported average length; cm)** | **Area** | ***K*** **(year$^{-1}$)** | ***L***$_\infty$ **(SCL; cm)** | ***W***$_\infty$ **(kg)** | **Sample size** | **Size range (cm)** | **Comments; reference [method]** |
|---|---|---|---|---|---|---|---|
| *Lepidochelys kempii* (56-79) | Gulf of Mexico | 0.317 | 62.3 | 24.4 | 117a | | Caillouet *et al.* (1995) [MR] |
| | Atlantic: Gulf of Mexico | 0.129 | 80.0 | 49.5 | 36 | 21.5–60.3 | Schmid & Witzell (1997) [MR] |
| | Atlantic: Cape Canaveral | 0.577 | 61.1 | 23.0 | 12c | 21.5-60.3 | Probably underestimated due to lack of adult sized Kemp's ridley turtles in the database; Schmid (1995) [MR] |
| | Atlantic: Cape Canaveral | 0.594 | 60.8 | 22.7 | 10 | 21.5-60.3 | 60% 20-40cm; probably underestimated due to lack of adult sized Kemp's ridley turtles in the database; Schmid (1995) [MR] |
| | Atlantic | 0.215 | 58.9 | 20.8 | 56 | | Zug et al. (1997) [SC] |
| | Gulf of Mexico | 0.219 | 70.5 | 34.6 | 15 | | Zug et al. (1997) [SC] |
| | Atlantic: Gulf of Mexico | 0.079 | 87.7 | 64.2 | 70 | | Zug et al. (1997) [SC] |
| | Gulf of Mexico: Cedar Keys | 0.085 | 91.4 | 72.2 | 24 | | Schmid (1998) [SC] |
| | Atlantic | 0.167 | 73.2 | 38.5 | 38 | | Turtle Expert Working Group (2000)b [SC, MR] |
| | Gulf of Mexico | 0.210 | 71.1 | 35.4 | 58 | | Turtle Expert Working Group (2000) [SC, MR] |
| | Atlantic | 0.115 | 74.9 | 41.0 | 109 | 21.7–50.5 | Snover *et al.* (2007) [SC] |
| | Gulf of Mexico | 0.053 | 97.0 | 85.4 | 660 | 20-61 | Bjorndal & Bolten (1997) [LF] |
| *Caretta caretta* (92) | Atlantic: Cape Canaveral | 0.059 | 96.1 | 118 | 51c | 38.2-110 | 80%<80 cm SCL; 20%>80cm; Schmid (1995) [MR - Adults include males and females] |
| | Atlantic: Cape Canaveral | 0.037 | 112 | 185 | 17 | 38.2–110 | Growth model for captures and recaptures by the contract vessel; size range for study but not specified for N=19; Schmid (1995) [MR] |
| | Chesapeake Bay | 0.076 | 112 | 182 | 83 | 13-42 | Klinger & Musick (1995) [SC] |
| | Atlantic (Florida, Georgia & South Carolina) | 0.031 | 110 | 174 | 118 | 45–110 | Size range for study, no specified for N=118; Henwood (1987) [MR] |
| | Azores, North Atlantic | 0.072 | 98.9 | 129 | 574 | 10-64 | Assuming 105.5 CCL, where CCL=1.388+(1.053)(SCLnt); Bjorndal *et al.* (2000b) [LF] |
| | Florida, Mosquito lagoon | 0.120 | 94.6 | 114 | 28 | 53.3-77.3 | Frazer & Ehrhart (1985) [MR] |
| | Florida | 0.115 | 94.7 | 114 | 41 | 53.3–77. | Size range based on 8 individuals with specified lengths, 20 adults with lengths not specified, and 13 individuals with no specified lengths but assumed <82 cm; Frazer (1987) [MR] |
| | North Carolina | 0.052 | 107 | 160 | 57 | 45.1–75.8 | Braun-McNeill *et al.* 2002 in Epperly *et al.*(2001) [MR] |

**Table A1**. Continued.

| Species (reported average length; cm) | Area | *K* (year$^{-1}$) | $L_\infty$ (SCL; cm) | $W_\infty$ (kg) | Sample size | Size range (cm) | Comments; reference [method] |
|---|---|---|---|---|---|---|---|
| *Caretta caretta* (92) | Florida | 0.064 | 96.7 | 121 | 54 | 62.2–104.2 | Foster (1994) [MR] |
| | Georgia, Cumberland island | 0.096 | 96.8 | 121 | 69 | >49.76-103 | Reported in CCL and converted to SCL using SCL=(0.948×CCL)–1.442 ; Teas (1993); Parham & Zug (1997) [SC–1979 ; regression growth protocol] |
| | Georgia, Cumberland island | 0.098 | 102 | 138 | 25 | >49.76–103 | Reported in CCL and converted to SCL using SCL=(0.948×CCL)–1.442 ; Teas (1993); Parham & Zug (1997) [SC–resampled 1979 data–correction factor protocol] |
| | Georgia, Cumberland island | 0.086 | 95.4 | 116 | 25 | >49.76–103 | Reported in CCL and converted to SCL using SCL=(0.948×CCL)–1.442 ; Teas (1993); Parham & Zug (1997) [SC–resampled 1979 data–regression growth protocol |
| | Georgia, Cumberland island | 0.106 | 108 | 163 | 26 | >36.04–103 | Parham & Zug (1997) [SC – 1980 correction factor protocol] |
| | Georgia, Cumberland island | 0.074 | 109 | 170 | 26 | >36.04–103 | Parham & Zug (1997) [SC – 1980 regression growth protocol] |
| | Gulf of Mexico | 0.051 | 106 | 155 | 570 | >36.04–103 | Bjorndal *et al* .(2001) [LF] |
| | Florida, Atlantic coast | 0.044 | 111 | 178 | 1234 | 42.2-81.03 | Reported in CCL and converted to SCL using SCL=(0.948×CCL)–1.442 ; Teas (1993); Bjorndal et al. (2001) [LF] |
| | Texas | 0.030 | 144 | 372 | 819 | 46-87 | Bjorndal & Bolten (1997) [LF] |
| | Great Barrier Reef, Australia | 0.060 | 105 | 151 | 172 | 63–90.3 | Reported in CCL and converted to SCL using SCL=(0.948×CCL)–1.442 ; Teas (1993); Frazer *et al.* (1994) [MR] |
| *Chelonia mydas* (91) | Florida, Mosquito lagoon | 0.089 | 109 | 157 | 11 | 27.7->69.6 | Frazer & Ehrhart (1985) [MR] |
| | Florida, Atlantic | 0.026 | 182 | 694 | 976 | 25-70 | Bjorndal & Bolten (1997) [LF] |
| | Inagua, Bahamas | 0.072 | 99.7 | 122 | 964 | 25-70 | Bjorndal & Bolten (1995) [LF] |
| | US Virgin Islands | 0.048 | 148 | 379 | 41 | 25.6–62.3 | Size range at first capture; Boulon & Frazer (1990) [MR] |
| | Watamu, Kenya | 0.068 | 117 | 195 | 563 | 31-108 | Reported in CCL and converted to SCL using SCL=0.932*CCL+0.369 ; Peckham *et al.* (2008) ; Watson (2006) [MR] |

**Table A1**. Continued.

| Species (reported average length; cm) | Area | *K* (year$^{-1}$) | *L∞* (SCL; cm) | *W∞* (kg) | Sample size | Size range (cm) | Comments; reference [method] |
|---|---|---|---|---|---|---|---|
| *Eretmochelys imbricata* (63-90) | St Thomas, Virgin islands | 0.071 | 100 | 88.9 | 9 | 36-43 | Boulon (1994) as in Heppell & Crowder (1996) [MR] |
| | Mona Island, Puerto Rico | 0.036 | 100 | 88.9 | 15 | - | Van Dam and Diez (1994) as in Heppell & Crowder (1996) [MR] |
| | Queensland, Australia | 0.048 | 100 | 88.9 | 41 | 33-82 | Reported in CCL and converted to SCL using SCL=SCL=0.935*CCL+0.449; Limpus (1992) as in Heppell & Crowder (1996) |

# A PRELIMINARY COMPILATION OF LIFE-HISTORY DATA FOR MEDITERRANEAN MARINE INVERTEBRATES[1]

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## ABSTRACT

Quantitative information on the life-history traits of fish is available online through FishBase (www.fishbase.org). This is not the case for marine invertebrates, although these organisms are of primary importance to marine ecosystems and are being heavily exploited. In order to fill this gap for the Mediterranean at least, we surveyed the primary and grey scientific literature and collected the following type of information on Mediterranean marine invertebrates: (i) length-weight relationships; (ii) maximum length ($L_{max}$) and age ($T_{max}$); (iii) length conversion relationships; (iv) von Bertalanffy growth parameters; and (v) length at maturity ($L_m$). Overall, we collected data for 246 stocks of 48 species belonging to 5 major groups (Decapoda, Bivalvia, Cephalopoda, Holothuroidea and Anthozoa). We established empirical relationships to predict asymptotic length ($L_\infty$) from $L_{max}$ and $L_m$ from $L_\infty$. Finally, we analyzed growth parameters using the auximetric plot at the group (Decapoda and Bivalves) and species level (*Aristaemorpha foliacea, Nephrops norvegicus and Plesionika martia*).

## INTRODUCTION

Growth parameters and length-weight relationships are important not only for theoretical aspects, e.g., life-history trade-offs (Binohlan & Pauly, 2000; Charnov, 1993), but for practical reasons as well, e.g., conservation and management. In addition, compilations of historical growth data are of paramount importance for establishing baselines (Pauly, 1995).

Compared to fish, invertebrate stocks are expected to be less vulnerable to overfishing, primarily due to their small body size (Jennings *et al.*, 1998). Yet, their high economic value, and thus the high fishing effort they experience, combined with the absence or low mobility of most invertebrate species, can change this (Thorpe *et al.*, 2006). In addition, many benthic invertebrates are keystone components for the Mediterranean ecosystems (Coll *et al.*, 2006; 2007). Growth parameters and length-weight relationships have been assembled for fishes from different aquatic ecosystems of the world and are available online through FishBase (www.fishbase.org, Froese & Pauly, 2008). Though various compilations exist for marine invertebrates (e.g., Relini *et al.*, 1999; Ramirez Llorda, 2002), they were done in a less systematic fashion than presented here, and are not available online (as the data presented here will be through SeaLifeBase, www.sealifebase.org).

In this report, we present a preliminary compilation of life-history data (i.e., maximum length and age, length-weight relationships, von Bertalanffy growth parameters and length at first maturity) for Mediterranean marine invertebrates (Decapoda, Cephalopoda, Bivalvia, Holothuroidea and Anthozoa). This complements previous collections of life-history data for Mediterranean fishes (see Stergiou & Karpouzi, 2002; Stergiou *et al.*, 2006), and will (i) allow the study and comparison of the patterns and propensities in the life-history of main organisms embedded in the Mediterranean; and (ii) facilitate the construction of ecosystem models of the Mediterranean Sea.

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## MATERIALS AND METHODS

We gathered peer-reviewed and grey literature (i.e., local journals, national and international conference proceedings, technical reports and theses) reporting growth parameters for Mediterranean marine invertebrates using the Aquatic Sciences and Fisheries Abstracts (ASFA), the Web of Science, and Google Scholar. We collected the following type of information (Table 1): (i) maximum age and length, $T_{max}$ (years) and $L_{max}$ (cm), respectively; (ii) length type reported (i.e., carapace length (CL); total length (TL); shell length (SHL); shell height (SHH); mantle length (ML); vertical length (VL)); (iii) morphometric relationships between CL and TL for Decapoda and SHL and SHH for Bivalvia; (iv) the parameters $a$ and $b$ of the length-weight relationship ($W=aL^b$) and length at maturity, $L_m$ (cm); and (v) the von Bertalanffy growth parameters, $L_\infty$ (cm), $K$ (year$^{-1}$) and $t_0$ (year), and the method used to estimate them. We also collected auxiliary information on the sampling characteristics (i.e., sampling gear, frequency, date and region and sample size).

In all cases, the parameter $a$ of the length-weight relationship was originally estimated by the authors using millimeters as length unit. We converted all estimates to cm using the formula $a'(cm) = a(mm)*10^b$ (Binohlan & Pauly, 1998; Stergiou & Moutopoulos, 2001). We presented $T_{max}$ only when it was estimated from growth rings (presumed to be annual), which applied to 11 bivalve stocks. When multiple methods were used by the original authors for the estimation of growth parameters, we selected the results of the method with the best fit.

We estimated the $L_{max}/L_\infty$ and $L_m/L_\infty$ ratios and established empirical relationships to predict $L_\infty$ from $L_{max}$ and $L_m$ from $L_\infty$. Growth parameters were plotted with a double logarithmic scale (i.e., through an auximetric plot, Pauly *et al.*, 1996) in order to view the relationships between $K$ and $L_\infty$ and compare growth patterns among different Mediterranean groups and species. For 11 records, $L_\infty$ was expressed in TL or SHH. For 3 out of these 11 records, we used the known morphometric relationships to convert from one length type to another. For 8 cases, no conversion equation was found; we excluded them from the analysis.

## RESULTS

Overall, our dataset is based on 102 publications, of which 60 (59%) were published in sources not covered by the Science Citation Index (SCI). Most of the information gathered refers to Spain (86 stocks), Italy (83 stocks) and Greece (45 stocks), followed by Algeria (14 stocks), Croatia and Tunisia (6 stocks each) and France and Portugal (3 stocks each) (Figure 1). In total, 92% of the collected information refers to the northern Mediterranean.

We collected growth parameters for 246 invertebrate stocks belonging to 48 species and 29 families (Table A1), representing 5 major groups: (i) Decapoda: 28 species (57%) and 202 stocks (82%); (ii) Bivalvia: 10 species (24%) and 27 stocks (12%); (iii) Cephalopoda: 5 species (10%) and 11 stocks (4%); (iv) Holothuroidea: 3 species (6%) and 3 stocks (1%); and (v) Anthozoa: 1 species (2%) and 1 stock. The best-studied species in terms of growth were *Aristeus antennatus* (43 stocks), followed by *Nephrops norvegicus* (30 stocks), and *Aristaeomorpha foliacea* (25 stocks) (Figure 2), all of which are highly-commercial species.

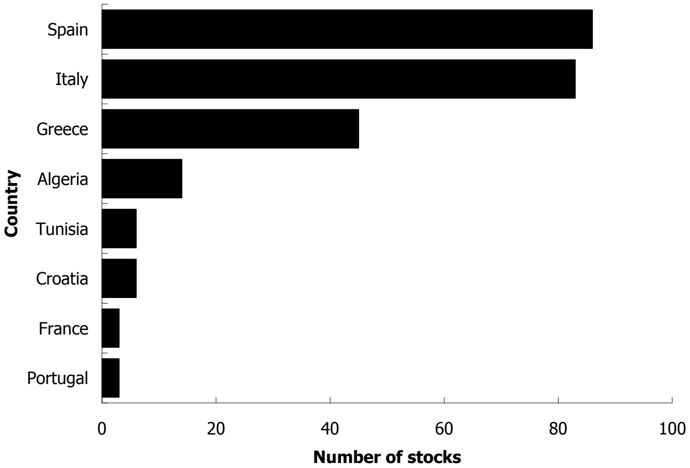

**Figure 1**. Distribution of growth information per Mediterranean country.

Sample size ranged from 10 individuals for *Holothuria sanctori* (Algeria) to 31,082 individuals for *Donax trunculus* (Southern Adriatic Sea) (Table A1). For 54% of the stocks for which there was available information on sampling frequency such information was derived from monthly (61%), seasonal (17%), yearly (2%) and bimonthly (2%)

sampling. For the remaining cases, either the sampling was irregular (16%), or the analysis was based on a single sample (3%). Information on the sampling gear was not available for 40% of the populations. For the remaining 60%, samples were mainly collected by trawling (79%) followed by other gears (22%) (i.e., scuba diving, hand dredges, lift nets, trammel nets, trawling box, etc.).

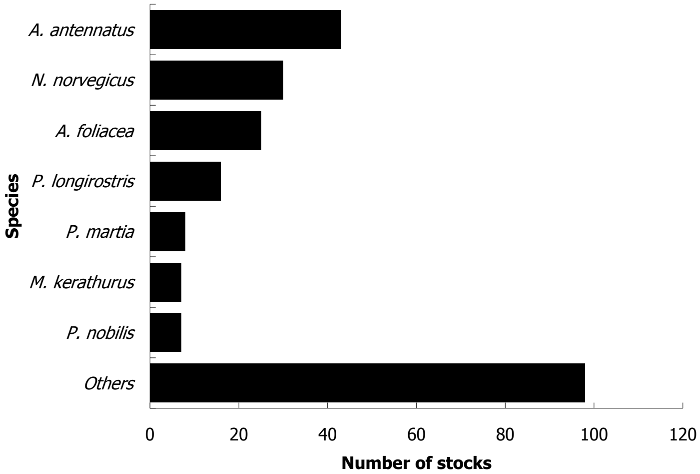

**Figure 2**. The best studied invertebrate species in the Mediterranean Sea.

Information on the ageing method was unavailable for 12% of the stocks (Table A1). For the remaining stocks, growth was studied using length-frequency analysis (91%), shell rings reading (7%) and tag-recapture data (2%). Length-frequency analysis was the only method used for the Decapoda, Cephalopoda and Holothuroidea. For the estimation of VBGF parameters, the ELEFAN software (Pauly, 1987) was used in 70% of the stocks followed by non-linear fitting of age-at-length data (24%). The method used for estimating the parameters of the VBGF was not available for 37% of the 246 cases.

The *K* parameter varied between 0.03 year$^{-1}$ for *Nephrops norvegicus* (Catalan Sea) and 2.06 year$^{-1}$ for *Palaemon adspersus* (Balearic Islands) (Figure 3). The mean *K* value for Decapoda and Bivalvia was 0.51 year$^{-1}$ (s.e. = 0.02; n = 31) and 0.52 year$^{-1}$ (s.e. = 0.02; n = 210) respectively, with the two means being significantly different (t-test; t = -2.957; P = 0.003).

Longevity ($T_{max}$) from growth readings reported for 11 Bivalve stocks (Table A1) ranged between 4 and 28 years for *Pinna nobilis* in Carboneras (Spain) and the Thermaikos Gulf (Greece) respectively. $L_{max}$ was reported for 146 invertebrate stocks (Decapoda: 126 stocks; Bivalves: 11 stocks; Cephalopoda: 6 stocks; and Holothuria: 3 stocks). The $L_{max}/L_{\infty}$ ratio ranged between 0.39 for *N. norvegicus* (Catalan sea) and 1.19 for *A. antennatus* (Ionian Sea), with a mean value of 0.88 (s.e. = 0.01).

The relationship between $L_{\infty}$ and $L_{max}$ was established for: (a) Decapoda: $logCL_{\infty} = 0.0471+1.0266logCL_{max}$ ($r^2$ = 0.93; n = 126; s.e.$_{slope}$ = 0.025; $P < 0.001$), (b) Bivalvia: $logSHL_{\infty} = 0.0708+0.9611logSHL_{max}$ ($r^2$ = 0.99; n = 11; s.e.$_{slope}$ = 0.038; $P < 0.001$), and (c) all stocks combined: $logL_{\infty} = 0.0653+0.9920logL_{max}$ ($r^2$ = 0.96; n = 146; s.e.$_{slope}$ = 0.016; $P < 0.001$).

Values of $L_m$ were also obtained for 29 Decapoda stocks (7 species), 2 Bivalvia stocks (2 species), and 3 Cephalopoda stocks (2 species). The $L_m/L_{\infty}$ ratio ranged between 0.30 for *A. antennatus* (Ibiza Channel, Spain) and 0.66 for *Melicertus kerathurus* (Amvrakikos Gulf, Greece), with a mean value of 0.48 (s.e. = 0.017). The relationship between $L_m$ and $L_{\infty}$ is presented in Figure 4.

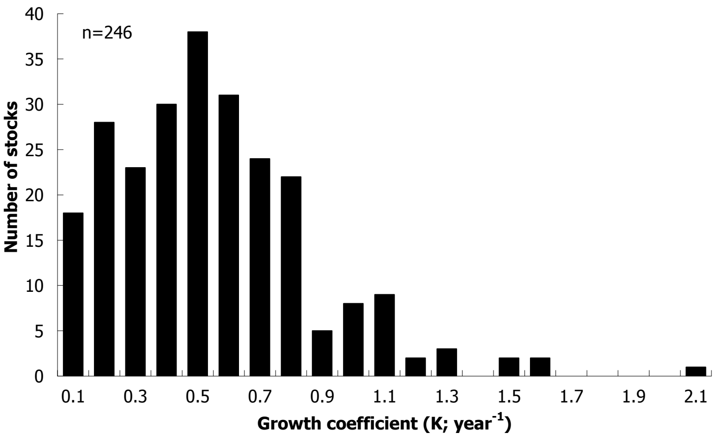

**Figure 3.** Distribution of *K* values for Mediterranean invertebrates.

Length-weight relationships were reported only for Decapoda (82 stocks and 23 species) and Bivalvia (10 stocks and 6 species). Length-weight relationships were reported only for 36% of the stocks (and 59% of the species) for which VBGF parameters were available. For Decapoda, *b* ranged between 1.4 for female *Sergestes arcticus* (Catalan Sea) and 3.82 for female *Polycheles typhlops* (Catalan Sea) (mean = 2.83; s.e. = 0.043). For bivalves, *b* ranged between 2.78 for *Chamelea gallina* (Adriatic Sea) and 3.33 for *Venus verrucosa* (Italy) (mean = 3.02; s.e. = 0.072).

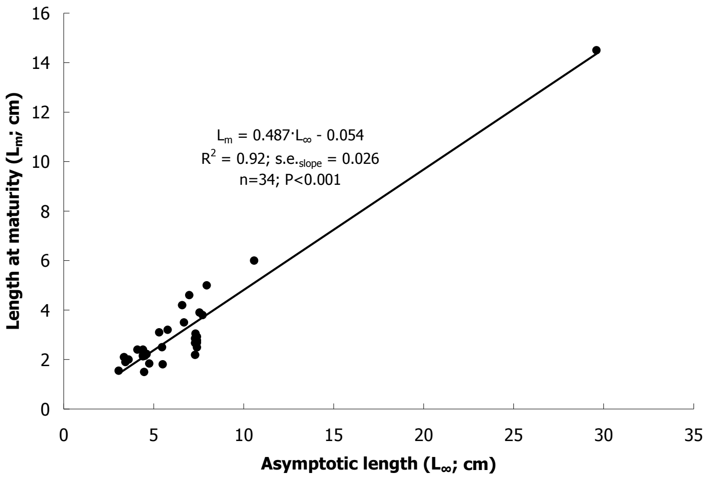

**Figure 4**. The relationship between length at maturity ($L_m$) and asymptotic length ($L_\infty$) for 34 Mediterranean marine invertebrate stocks

We also gathered 7 morphometric relationships for 7 stocks and 5 species of Mediterranean invertebrates, useful for the conversion of SHL and TL into SHH and CL, respectively, and vice versa (Table A1). Auximetric analysis was based on 194 and 29 sets of growth parameters for Decapoda and Bivalvia, respectively, but was not performed for groups represented by few cases (i.e., Cephalopoda, Holothuroidea, and Anthozoa) (Figure 5).

**Table 1**. Auximetric relationships for 3 Mediterranean invertebrate species.

| **Species** | **n** | **Relationship** | **$r^2$** | **s.e.$_{slope}$** | **P** |
|---|---|---|---|---|---|
| *Aristaeomorpha foliacea* | 25 | $\log k = 0.124 - 0.533 \log CL_\infty$ | 0.207 | 0.218 | 0.022 |
| *Nephrops norvegicus* | 30 | $\log k = 0.225 - 1.336 \log CL_\infty$ | 0.664 | 0.180 | <0.001 |
| *Plesionika martia* | 8 | $\log k = 0.416 - 1.590 \log CL_\infty$ | 0.758 | 0.367 | 0.005 |

The same was true for *Mytilus galloprovincialis* ($L_\infty$ = 12.5, $K$ = 0.048, Ligurian Sea) and *P. nobilis* ($L_\infty$ = 67.13, $K$ = 0.006, Mar Menor Lagoon). The plots revealed a significant negative linear relationship for both Decapoda and Bivalvia, the former with a steeper slope (Figure 5). The two slopes were significantly different at the 0.05 level (ANCOVA, P=0.0175).

Auximetric relationships were estimated for *A. foliacea*, *N. norvegicus* and *Plesionika martia* (Table 1). This was not done for the rest where a low number of growth parameters were available (n<4) or the relationship was statistically not significant (P>0.05).

## DISCUSSION

Most of the species presented in our compilation are either of high commercial value or are discards of Mediterranean fisheries (Machias *et al.*, 2001; Sanchez *et al.*, 2004; Gokce *et al.*, 2007). Concerning the articles collected, 41% were derived from SCI journals and the remaining from grey literature sources. This is very close to what was reported by Stergiou & Tsikliras (2006) for Mediterranean fishes, indicating the importance of the grey literature in the study of Mediterranean marine ecosystems. In addition, biological information on Mediterranean invertebrates is not equally distributed geographically, i.e., southern Mediterranean countries are strongly underrepresented.

Marine invertebrates are a very diverse group. This diversity is also reflected in the various length types reported (i.e., CL, ML, SHL), which highlights the importance of conversion equations in order for comparisons to be done. All empirical relationships presented here displayed a strong fit and were in accordance with similar relationships estimated for fish (e.g., Froese & Binohlan, 2000). The only exception was the high slope (1.027) of the $L_\infty$-$L_{max}$ relationship for Decapoda, probably reflecting the underestimation of $L_\infty$ for organisms with small body size (Froese & Binohlan, 2000). The $L_{max}/L_\infty$ ratio, which had a mean value of 0.88 (s.e. = 0.01), is similar to that reported by Stergiou (2000) for Greek marine fishes. The highly significant relationships between $L_\infty$ and $L_{max}$ and $L_m$ and $L_\infty$ can be used to predict $L_\infty$ and $L_m$ for less studied species or stocks in data-poor situations such as in the southern Mediterranean.

With respect to the $K$-$L_\infty$ relationships, the intercept cannot be compared across groups because of the different length types used. However, slopes are comparable and the slope for Decapoda was found to be steeper than for Bivalvia (0.36) and for Mediterranean fishes (0.39, n=1029, Apostolidis & Stergiou unpublished data). This relationship is known as the growth trade-off and the slope has been related to other life-history parameters and has a metabolic basis (Charnov, 1993; 2007). In addition, the slopes for the 3 invertebrate species presented here are higher than those of the groups in which these species belong (see Charnov, 1993).

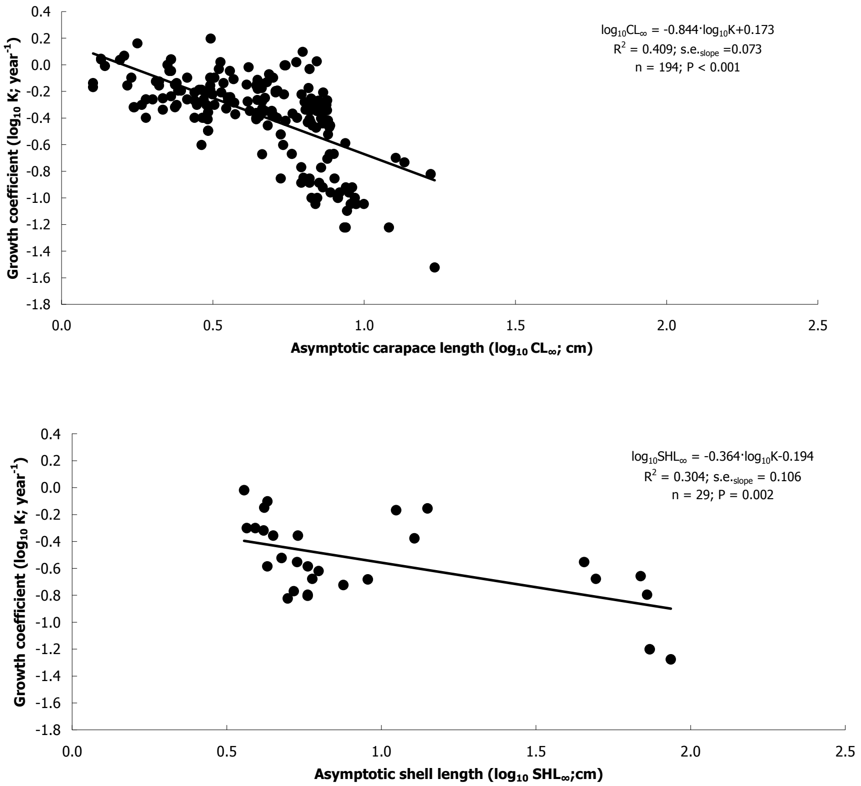

**Figure 5**. Relationship between growth coefficient (*K*) and asymptotic length ($L_\infty$) for decapod crustaceans (upper panel) and and bivalve mollusks (lower panel).

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**Table A1**. Life history parameters of Mediterranean invertebrates. N denotes the sample size. S denotes sex, i.e., F: female; M: male; and C: combined. Length-based parameters, i.e., asympotic length ($L_\infty$), length at maturity ($L_m$) and maximum length ($L_{max}$) are in cm. The growth coefficient ($K$) is in year$^{-1}$ and $t_0$ in year. Length-weight relationship coefficients $a$ and $b$ dimensionless. AM denotes the ageing method of original data set (LF: length frequency analysis; T: tag-recapture data; SR: shell rings readings) and M denotes the method used for the estimation of the von Bertalanffy growth parameters (NL: non-linear estimation; El: Elefan software; GH: Gulland-Holt plot; FW: Ford-Walford plot).

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Decapoda** | | | | | | | | | | | | | | | | |
| *Aristaeomorpha foliacea* | Italy | C. Tyrrhenian Sea | - | F | 7.32 | 0.620 | 0.19 | - | - | 3.05 | - | - | LF | - | CL | Leonardi & Ardizzone (1994; in Spedicato *et al.*, 1999a) |
| | | Tyrrhenian Sea | - | F | 7.32 | 0.483 | -0.44 | 0.5241 | 2.69 | - | - | - | LF | - | CL | Spedicato *et al.* (1998; in Spedicato *et al.*, 1999a) |
| | | S. Tyrrhenian Sea | - | F | 7.10 | 0.470 | -0.28 | - | - | - | - | - | - | - | CL | Spedicato *et al.* (1994; in Papaconstantinou & Kapiris 2003) |
| | | Sardinian Channel | - | F | 5.10 | 0.620 | 0.00 | - | - | - | - | - | - | - | CL | Mura *et al.* (1997; in Papaconstantinou & Kapiris 2003) |
| | | Sardinian Channel | - | M | 5.10 | 0.635 | - | - | - | - | - | - | - | - | CL | Mura *et al.* (1997; in Papaconstantinou & Kapiris 2003) |
| | | Sardinian Sea | - | F | 7.54 | 0.456 | 0.58 | - | - | 3.90 | - | - | LF | - | CL | Cau *et al.* (1994; in Spedicato *et al.*, 1999a) |
| | | Sicilian Channel | - | F | 6.55 | 0.670 | 0.00 | - | - | - | - | 7.00 | LF | - | CL | Ragonese *et al.* (1994; in Spedicato *et al.*, 1999a) |
| | | Sicilian Channel | - | M | 4.15 | 0.960 | 0.28 | - | - | - | - | - | LF | - | CL | Ragonese *et al.* (1994; in Papaconstantinou & Kapiris 2003) |
| | | Sicilian Channel | - | F | 6.58 | 0.520 | -0.23 | - | - | 4.20 | - | - | - | - | CL | Ragonese *et al.* (2004) |
| | | Ionian Sea | - | F | 6.98 | 0.450 | -0.18 | - | - | - | - | 6.50 | LF | - | CL | Matarrese *et al.* (1997; in Spedicato *et al.*, 1999a) |
| | | Ionian Sea | - | F | 6.98 | 0.450 | -0.18 | - | - | - | - | 6.90 | LF | - | CL | Tursi *et al.* (1998; in Fiorentino, 2000) |
| | | Ionian Sea | - | M | 4.97 | 0.420 | -0.34 | - | - | - | - | 4.40 | LF | - | CL | Tursi *et al.* (1998; in Fiorentino, 2000) |
| | | W. Ionian Sea | 295 | F | 6.60 | 0.450 | - | - | - | - | - | 6.50 | LF | - | CL | D'Onghia *et al.* (1998a; in Politou *et al.*, 2004) |
| | | W. Ionian Sea | 386 | M | 5.00 | 0.420 | - | - | - | - | - | 4.50 | LF | - | CL | D'Onghia *et al.* (1998a; in Politou *et al.*, 2004) |
| | | Tyrrhenian Sea | 20819 | C | 7.20 | 0.396 | 0.00 | - | - | - | - | 7.20 | LF | NL | CL | Cau *et al.* (2002) |
| | | Sardinian Sea | 14660 | C | 7.07 | 0.538 | 0.27 | - | - | - | - | 7.00 | LF | NL | CL | Cau *et al.* (2002) |
| | Greece | Aegean Sea | 1963 | C | 6.21 | 0.600 | -0.34 | - | - | - | - | 6.00 | LF | NL | CL | Cau *et al.* (2002) |
| | | N.E. Ionian Sea | - | F | 7.25 | 0.430 | - | - | - | - | - | 7.00 | LF | - | CL | Anonymous (2001; in Politou *et al.*, 2004) |
| | | N.E. Ionian Sea | - | M | 6.00 | 0.400 | - | - | - | - | - | 5.90 | LF | - | CL | Anonymous (2001; in Politou *et al.*, 2004) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aristaeomorpha foliacea* | Greece | Aegean Sea | 1963 | C | 6.21 | 0.600 | -0.34 | - | - | - | - | 6.00 | LF | NL | CL | Cau *et al.* (2002) |
| | | N.E. Ionian Sea | - | F | 7.25 | 0.430 | - | - | - | - | - | 7.00 | LF | - | CL | Anonymous (2001; in Politou *et al.*, 2004) |
| | | N.E. Ionian Sea | - | M | 6.00 | 0.400 | - | - | - | - | - | 5.90 | LF | - | CL | Anonymous (2001; in Politou *et al.*, 2004) |
| | | E. Ionian Sea | 392 | F | 6.66 | 0.370 | - | - | - | - | - | 6.20 | LF | NL | CL | Politou *et al.* (2004) |
| | | E. Ionian Sea | 498 | M | 4.70 | 0.450 | - | - | - | - | - | 5.10 | LF | NL | CL | Politou *et al.* (2004) |
| | | E. Ionian Sea | - | F | 6.40 | 0.460 | -0.19 | - | - | - | - | 6.20 | LF | EL | CL | Papaconstantinou & Kapiris (2003) |
| | | E. Ionian Sea | - | M | 4.70 | 0.564 | -0.13 | - | - | - | - | 4.00 | LF | EL | CL | Papaconstantinou & Kapiris (2003) |
| | Algeria | Algerian Coasts | - | F | 6.90 | 0.505 | - | - | - | - | - | 6.70 | LF | - | CL | Yahiaoui *et al.* (1994; in Politou *et al.*, 2004) |
| | | Algerian Coasts | - | M | 4.45 | 0.660 | - | - | - | - | - | 4.50 | LF | - | CL | Yahiaoui *et al.* (1994; in Politou *et al.*, 2004) |
| *Aristeus antennatus* | Spain | Ibiza Channel | - | F | 7.30 | 0.363 | -0.41 | 0.7323 | 2.48 | 2.19 | - | 5.90 | LF | EL | CL | García-Rodriguez & Esteban (1999) |
| | | Ibiza Channel | - | M | 5.50 | 0.380 | -0.43 | 0.7928 | 2.40 | 1.81 | - | 3.70 | LF | EL | CL | García-Rodriguez & Esteban (1999) |
| | | Catalan Sea | - | F | 7.60 | 0.300 | -0.07 | - | - | - | - | 6.10 | LF | EL | CL | Demestre (1990; in Company & Sardá, 2000) |
| | | Catalan Sea | - | M | 5.40 | 0.250 | - | - | - | - | - | 3.80 | LF | EL | CL | Demestre (1990; in Company & Sardá, 2000) |
| | | Algerian Coasts | 6962 | C | 7.60 | 0.382 | 0.20 | - | - | - | - | 4.40 | LF | NL | CL | Cau *et al.* (2002) |
| | | Murcia | - | F | 7.30 | 0.390 | -0.08 | - | - | - | - | - | - | - | CL | Martínez-Baños (1996; in Orsi Relini & Relini, 1998) |
| | | Balearic Islands | 5844 | F | 7.40 | 0.380 | - | 0.7628 | 2.42 | 2.93 | - | 6.10 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 1792 | M | 4.60 | 0.468 | - | 0.7730 | 2.32 | 2.23 | - | 3.80 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 2765 | F | 7.30 | 0.521 | - | 0.7083 | 2.47 | 2.67 | - | 6.10 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 1464 | M | 4.40 | 0.435 | - | 0.7365 | 2.42 | 2.15 | - | 3.80 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 2678 | F | 7.30 | 0.364 | - | 0.7657 | 2.44 | 2.85 | - | 6.00 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 1052 | M | 4.50 | 0.410 | - | 0.7789 | 2.36 | 2.15 | - | 3.70 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 1910 | F | 7.40 | 0.521 | - | 0.5480 | 2.46 | 2.78 | - | 6.30 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 961 | M | 4.40 | 0.390 | - | 0.7610 | 2.39 | 2.18 | - | 3.60 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 2291 | F | 7.40 | 0.510 | - | 0.7083 | 2.47 | 2.49 | - | 6.50 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 908 | M | 4.60 | 0.531 | - | 0.7676 | 2.38 | 2.21 | - | 3.50 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 4049 | F | 7.40 | 0.387 | - | 0.7378 | 2.47 | 2.69 | - | 6.40 | LF | EL | CL | Carbonell *et al.* (1999) |
| | | Balearic Islands | 1784 | M | 4.40 | 0.400 | - | 0.7836 | 2.35 | 2.13 | - | 3.60 | LF | EL | CL | Carbonell *et al.* (1999) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aristeus antennatus* | Italy | Ligurian Sea | - | F | 6.30 | 0.142 | 5.26 | - | - | - | - | - | LF | EL | CL | Orsi Relini & Relini (1985) |
| | | Ligurian Sea | - | F | 7.70 | 0.213 | -0.02 | - | - | - | - | 7.10 | LF | - | CL | Orsi Relini & Relini (1998a) |
| | | Ligurian Sea | - | M | 4.60 | 0.213 | -0.02 | - | - | - | - | - | LF | - | CL | Orsi Relini & Relini (1998b) |
| | | Tyrrhenian Sea | - | F | 6.68 | 0.558 | -0.23 | 0.7424 | 2.48 | 3.50 | - | 6.31 | LF | - | CL | Spedicato *et al.* (1995; in Spedicato *et al.*, 1999b) |
| | | Tyrrhenian Sea | - | F | 8.67 | 0.258 | - | - | - | - | - | 6.60 | LF | - | CL | Arculeo *et al.* (1994; in Spedicato *et al.*, 1999b) |
| | | Tyrrhenian Sea | - | - | 6.94 | 0.337 | - | - | - | - | - | - | LF | - | CL | Arculeo *et al.* (1994; in Spedicato *et al.*, 1999b) |
| | | Sardinian Sea | - | F | 7.68 | 0.340 | 0.37 | - | - | - | - | - | LF | - | CL | Cau *et al.* (1994; in Spedicato *et al.*, 1999b) |
| | | Sicilian Channel | 798 | F | 6.91 | 0.532 | 0.00 | - | - | - | - | 6.60 | LF | EL | CL | Ragonese & Bianchini (1996) |
| | | Ionian Sea | - | F | 7.72 | 0.350 | -0.36 | - | - | 3.80 | - | - | LF | - | CL | Matarrese *et al.* (1997; in Spedicato *et al.*, 1999b) |
| | | Ionian Sea | - | M | 5.46 | 0.990 | -0.14 | - | - | 2.50 | - | 6.50 | LF | - | CL | D'Onghia *et al.* (1994; in Spedicato *et al.*, 1999b) |
| | | Tyrrhenian Sea | - | F | 6.77 | 0.490 | 0.00 | - | - | - | - | - | LF | - | CL | Colloca *et al.* (1998; in Spedicato *et al.*, 1999b) |
| | | Ionian Sea | - | F | 6.60 | 0.930 | - | - | - | - | - | - | - | - | CL | Matarrese *et al.* (1992; in Papaconstantinou & Kapiris, 2001) |
| | | Ionian Sea | - | M | 5.50 | 0.990 | - | - | - | - | - | - | - | - | CL | Matarrese *et al.* (1992; in Papaconstantinou & Kapiris, 2001) |
| | | Ionian Sea | - | F | 7.72 | 0.350 | -0.36 | - | - | - | - | 6.60 | LF | - | CL | Tursi *et al.* (1998; in Fiorentino, 2000) |
| | | Ionian Sea | - | M | 5.15 | 0.400 | -0.35 | - | - | - | - | 3.90 | LF | - | CL | Tursi *et al.* (1998; in Fiorentino, 2000) |
| | | Tyrrhenian Sea | 8834 | C | 7.56 | 0.197 | -0.29 | - | - | - | - | 6.40 | LF | NL | CL | Cau *et al.* (2002) |
| | | Sardinian Sea | 9452 | C | 7.94 | 0.214 | -0.08 | - | - | - | - | 6.30 | LF | NL | CL | Cau *et al.* (2002) |
| | | Sicilian Channel | - | C | 6.91 | 0.532 | - | - | - | - | - | 6.60 | LF | - | CL | Levi *et al.* (1998; in Cau *et al.*, 2002) |
| | Greece | E. Ionian Sea | 7273 | F | 6.60 | 0.390 | 0.38 | 1.2835 | 2.05 | - | - | 6.20 | LF | EL | CL | Papaconstantinou & Kapiris (2001) |
| | | E. Ionian Sea | 1345 | M | 5.80 | 0.430 | -0.46 | 1.2216 | 2.06 | - | - | 4.50 | LF | EL | CL | Papaconstantinou & Kapiris (2001) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aristeus antennatus* | Algeria | - | - | F | 6.51 | 0.370 | 0.05 | - | - | - | - | - | - | - | CL | Yahiaoui *et al.* (1986; in Fiorentino, 2000) |
| | | Algerian Coasts | - | F | 6.75 | 0.350 | - | - | - | - | - | - | LF | - | CL | Nouar (2001) |
| | | Algerian Coasts | - | M | 3.75 | 0.425 | - | - | - | - | - | - | LF | - | CL | Nouar (2001) |
| | France | Lion Gulf | - | F | 6.36 | 0.525 | -0.26 | - | - | - | - | - | - | - | CL | Campillo (1994; in Orsi Relini & Relini, 1998) |
| | Portugal | Algarve | - | F | 7.54 | 0.360 | -0.30 | - | - | - | - | - | - | - | CL | Dos Santos & Cascalho (1994; in Orsi Relini & Relini, 1998) |
| *Chlorotocus crassicornis* | Greece | N. Aegean Sea | 201 | F | 1.90 | 0.400 | -0.30 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | N. Aegean Sea | 164 | M | 1.74 | 0.480 | -0.27 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | N. Aegean Sea | 365 | C | 1.73 | 0.480 | -0.31 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| *Geryon longipes* | Spain | Catalan Sea | 203 | F | 5.30 | 0.300 | - | 0.4224 | 3.14 | - | - | 4.91 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 35 | M | 7.50 | 0.500 | - | 0.4121 | 3.20 | - | - | 6.97 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 238 | C | 7.55 | 0.540 | - | 0.4620 | 3.10 | - | - | 6.97 | LF | EL | CL | Company & Sardá (2000) |
| *Medorippe lanata* | Italy | E. Ligurian Sea | 725 | F | 3.35 | 1.050 | - | - | - | 2.10 | - | 2.90 | LF | EL | CL | Rossetti *et al.* (2006) |
| | | E. Ligurian Sea | 639 | M | 3.11 | 1.575 | - | - | - | - | - | 2.90 | LF | EL | CL | Rossetti *et al.* (2006) |
| *Melicertus kerathurus* | Greece | Amvrakikos Gulf | - | F | 24.74 | 0.572 | -0.30 | - | - | - | - | - | LF | FW | TL | Conides *et al.* (1990; in Stergiou *et al.*, 1997) |
| | | Amvrakikos Gulf | - | M | 24.17 | 0.470 | -0.37 | - | - | - | - | - | LF | FW | TL | Conides *et al.* (1990; in Stergiou *et al.*, 1997) |
| | | Amvrakikos Gulf | - | F | 6.97 | 1.062 | 0.24 | - | - | 4.60 | - | 6.20 | LF | NL | CL | Conides *et al.* (2006) |
| | | Amvrakikos Gulf | - | M | 6.27 | 1.253 | - | - | - | - | - | - | LF | NL | CL | Conides *et al.* (2006) |
| | | Amvrakikos Gulf | 5505 | C | 5.97 | 1.047 | - | - | - | - | - | 6.20 | LF | NL | CL | Conides *et al.* (2006) |
| | Tunisia | Gabes Gulf | - | F | 5.43 | 0.600 | -0.86 | - | - | - | - | - | LF | - | CL | Ben Meriem (2004) |
| | | Gabes Gulf | - | M | 3.70 | 0.780 | -0.96 | - | - | - | - | - | LF | - | CL | Ben Meriem (2004) |
| *Munida intermedia* | Spain | Catalan Sea | 55 | F | 2.9 | 0.250 | - | 0.8494 | 3.31 | - | - | 2.72 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 76 | M | 3.05 | 0.320 | - | 0.9093 | 3.06 | - | - | 2.87 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 131 | C | 3.05 | 0.320 | - | 0.8712 | 3.23 | - | - | 2.87 | LF | EL | CL | Company & Sardá (2000) |
| | Italy | C. Adriatic Sea | - | F | 2.16 | 0.460 | -0.76 | 1.0715 | 2.96 | - | - | 2.30 | LF | NL | CL | Gramitto & Froglia (1998) |
| | | C. Adriatic Sea | - | M | 2.37 | 0.480 | -0.59 | 1.0233 | 3.23 | - | - | 2.50 | LF | NL | CL | Gramitto & Froglia (1998) |
| *Munida tenuimana* | Spain | Catalan Sea | 61 | F | 2.75 | 0.400 | - | 0.6805 | 3.14 | - | - | 2.51 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 67 | M | 2.92 | 0.400 | - | 0.6540 | 3.15 | - | - | 2.60 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 128 | C | 2.95 | 0.400 | - | 0.6794 | 3.15 | - | - | 2.60 | LF | EL | CL | Company & Sardá (2000) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Nephrops norvegicus* | Italy | E. Ligurian Sea | - | F | 5.77 | 0.214 | 0.00 | - | - | 3.20 | - | - | LF | NL | CL | Abella & Righini (1998) |
| | | E. Ligurian Sea | - | M | 7.21 | 0.169 | 0.00 | - | - | - | - | - | LF | NL | CL | Abella & Righini (1998) |
| | | Sicilian Channel | - | F | 5.30 | 0.140 | -0.50 | 0.5935 | 3.13 | 3.10 | - | - | - | - | CL | Ragonese *et al.* (2004) |
| | | Sicilian Channel | - | M | 6.20 | 0.130 | -0.50 | 0.3072 | 2.86 | - | - | - | - | - | CL | Ragonese *et al.* (2004) |
| | | Ligurian Sea | 37 | F | 7.74 | 0.110 | -1.32 | - | - | - | - | 5.50 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Ligurian Sea | 32 | M | 8.90 | 0.110 | -1.08 | - | - | - | - | 6.30 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Tyrrhenian Sea | 46 | F | 8.78 | 0.080 | -1.26 | - | - | - | - | 6.00 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Tyrrhenian Sea | 61 | M | 9.98 | 0.090 | -1.39 | - | - | - | - | 7.50 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Adriatic Sea | 30 | F | 8.18 | 0.100 | -1.36 | - | - | - | - | 5.40 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Adriatic Sea | 88 | M | 12.08 | 0.060 | -1.92 | - | - | - | - | 6.50 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | Spain | Alboran Sea | 49 | F | 9.39 | 0.090 | -1.61 | - | - | - | - | 4.80 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Alboran Sea | 39 | M | 9.13 | 0.120 | -1.08 | - | - | - | - | 6.00 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Catalan Sea | 38 | F | 17.11 | 0.030 | -1.80 | - | - | - | - | 6.60 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Catalan Sea | 40 | M | 9.42 | 0.090 | -0.81 | - | - | - | - | 7.90 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Catalan Sea | - | F | 7.00 | 0.100 | -2.07 | - | - | - | - | - | LF | EL | CL | Sardá & Lleonart (1993) |
| | | Catalan Sea | - | M | 8.20 | 0.100 | -0.69 | - | - | - | - | - | LF | EL | CL | Sardá & Lleonart (1993) |
| | Greece | Euboikos Gulf | 79 | F | 9.03 | 0.090 | -1.27 | - | - | - | - | 5.20 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | Euboikos Gulf | 79 | M | 9.32 | 0.100 | -1.10 | - | - | - | - | 6.30 | LF | NL | CL | Mytilineou *et al.* (1998) |
| | | W.C. Aegean Sea | - | F | 6.90 | 0.090 | - | - | - | - | - | - | LF | EL | CL | Mytilineou *et al.* (1993; in Stergiou *et al.*, 1997) |
| | | W.C. Aegean Sea | - | M | 8.60 | 0.060 | - | - | - | - | - | - | LF | EL | CL | Mytilineou *et al.* (1993; in Stergiou *et al.*, 1997) |
| | | E.C. Aegean Sea | - | F | 6.70 | 0.100 | - | - | - | - | - | - | LF | EL | CL | Mytilineou *et al.* (1993; in Stergiou *et al.*, 1997) |
| | | E.C. Aegean Sea | - | M | 8.70 | 0.060 | - | - | - | - | - | - | LF | EL | CL | Mytilineou *et al.* (1993; in Stergiou *et al.*, 1997) |
| | | Thracian Sea | - | F | 6.60 | 0.140 | - | - | - | - | - | 5.50 | LF | EL | CL | Papaconstantinou *et al.* (1994; in Stergiou *et al.*, 1997) |
| | | Thracian Sea | - | M | 7.30 | 0.120 | - | - | - | - | - | 6.60 | LF | EL | CL | Papaconstantinou *et al.* (1994; in Stergiou *et al.*, 1997) |
| | | Toroneos & Siggitikos Gulfs | - | F | 6.60 | 0.130 | - | - | - | - | - | 5.30 | LF | EL | CL | Papaconstantinou *et al.* (1994; in Stergiou *et al.*, 1997) |
| | | Toroneos & Siggitikos Gulfs | - | M | 8.30 | 0.110 | - | - | - | - | - | 7.20 | LF | EL | CL | Papaconstantinou *et al.* (1994; in Stergiou *et al.*, 1997) |
| | Algeria | Beni-saf | - | F | 6.20 | 0.170 | - | - | - | - | - | - | LF | - | CL | Djabali *et al.* (1990) |
| | | Beni-saf | - | M | 7.98 | 0.140 | - | - | - | - | - | - | LF | - | CL | Djabali *et al.* (1990) |
| | | Beni-saf | - | F | 7.10 | 0.130 | - | - | - | - | - | - | LF | - | CL | Djabali *et al.* (1990) |
| | | Beni-saf | - | M | 8.70 | 0.120 | - | - | - | - | - | - | LF | - | CL | Djabali *et al.* (1990) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Palaemon adspersus* | Greece | Messolongi Lagoon | - | F | 7.90 | 0.165 | - | - | - | - | - | 6.30 | LF | FW | TL | Klaoudatos & Tsevis (1987; in Stergiou *et al.*, 1997) |
| | | Messolongi Lagoon | - | M | 6.50 | 0.165 | - | - | - | - | - | 6.00 | LF | FW | TL | Klaoudatos & Tsevis (1987; in Stergiou *et al.*, 1997) |
| | Spain | Balearic Islands | 2506 | F | 4.78 | 2.065 | - | 0.0186 | 2.96 | - | - | - | LF | GH | TL | Manent & Abella-Gutiérrez (2006) |
| | | Balearic Islands | 888 | M | 3.41 | 1.076 | - | 0.0160 | 3.01 | - | - | - | LF | GH | TL | Manent & Abella-Gutiérrez (2006) |
| *Palinurus elephas* | Italy | Corsica | - | F | 16.60 | 0.151 | -0.35 | - | - | - | - | - | T | - | CL | Marin (1985; in Secci & Cau, 1999) |
| | | Corsica | - | M | 13.59 | 0.185 | -0.34 | - | - | - | - | - | T | - | CL | Marin (1985; in Secci & Cau, 1999) |
| *Parapenaeus longirostris* | Italy | C.Tyrrhenian Sea | - | F | 4.44 | 0.740 | -0.13 | - | - | - | - | - | LF | - | CL | Ardizzone *et al.* (1990; in Tursi *et al.*, 1999) |
| | | C.Tyrrhenian Sea | - | M | 3.31 | 0.930 | -0.05 | - | - | - | - | - | LF | - | CL | Ardizzone *et al.* (1990; in Tursi *et al.*, 1999) |
| | | Sicilian Channel | - | C | 3.05 | 0.630 | -0.19 | 1.1340 | 2.27 | - | - | - | LF | EL | CL | Levi *et al.* (1995) |
| | | Sicilian Channel | - | F | 4.09 | 0.710 | - | - | - | 2.40 | - | - | - | - | CL | Ragonese *et al.* (2004) |
| | | Sicilian Channel | - | M | 3.43 | 0.730 | - | - | - | 1.90 | - | - | - | - | CL | Ragonese *et al.* (2004) |
| | | Tyrrhenian Sea | - | C | 4.59 | 0.670 | -0.25 | - | - | - | - | - | LF | - | CL | Carbonara *et al.* (1998; in Tursi *et al.*, 1999) |
| | | Tyrrhenian Sea | - | C | 5.17 | 0.640 | - | - | - | - | - | - | LF | - | CL | Carbonara *et al.* (1998; in Tursi *et al.*, 1999) |
| | | Tyrrhenian Sea | - | C | 4.61 | 0.720 | - | - | - | - | - | - | LF | - | CL | Carbonara *et al.* (1998; in Tursi *et al.*, 1999) |
| | | Ionian Sea | - | F | 4.77 | 0.740 | -0.19 | - | - | - | - | - | LF | - | CL | D'Onghia *et al.* (1998b; in Tursi *et al.*, 1999) |
| | | Ionian Sea | - | M | 3.55 | 0.540 | -0.19 | - | - | - | - | - | LF | - | CL | D'Onghia *et al.* (1998b; in Tursi *et al.*, 1999) |
| | Greece | Greek Seas | - | F | 3.72 | 0.520 | -0.30 | - | - | - | - | - | LF | - | CL | Anonymous (1999; in Sombrino *et al.*, 2005) |
| | | Greek Seas | - | M | 3.37 | 0.620 | -0.16 | - | - | - | - | - | LF | - | CL | Anonymous (1999; in Sombrino *et al.*, 2005) |
| | Portugal | Algarve | - | F | 4.40 | 0.700 | -0.30 | 1.1230 | 2.31 | 2.40 | - | - | LF | - | CL | Ribeiro-Cascalho (1988; in Sombrino *et al.*, 2005) |
| | | Algarve | - | M | 3.60 | 0.900 | -0.30 | 1.1616 | 2.19 | 2.00 | - | - | LF | - | CL | Ribeiro-Cascalho (1988; in Sombrino *et al.*, 2005) |
| | Algeria | Algerian Coasts | - | F | 4.44 | 0.545 | - | - | - | - | - | - | LF | - | CL | Nouar (2001) |
| | | Algerian Coasts | - | M | 3.55 | 0.570 | - | - | - | - | - | - | LF | - | CL | Nouar (2001) |
| *Pasiphaea multidentata* | Spain | Catalan Sea | 161 | F | 4.85 | 0.850 | - | 0.3157 | 2.61 | - | - | 4.67 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 276 | M | 4.44 | 0.770 | - | 0.3096 | 2.65 | - | - | 4.27 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 650 | C | 5.00 | 0.800 | - | 0.2511 | 2.84 | - | - | 4.67 | LF | EL | CL | Company & Sardá (2000) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pasiphaea sivado* | Spain | Catalan Sea | 144 | F | 2.60 | 0.550 | - | 0.1988 | 2.92 | - | - | 2.32 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 4156 | M | 2.75 | 0.620 | - | 0.2106 | 2.76 | - | - | 2.43 | LF | EL | CL | Company *et al.* (2001) |
| | | Catalan Sea | 276 | C | 2.95 | 0.550 | - | 0.2307 | 2.68 | - | - | 2.43 | LF | EL | CL | Company & Sardá (2000) |
| *Plesionika acanthonotus* | Spain | Catalan Sea | 64 | F | 1.90 | 0.550 | - | 0.9239 | 2.55 | - | - | 1.79 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 121 | M | 1.84 | 0.500 | - | 0.8203 | 2.97 | - | - | 1.62 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 192 | C | 1.90 | 0.550 | - | 0.7757 | 3.13 | - | - | 1.79 | LF | EL | CL | Company & Sardá (2000) |
| *Plesionika antigai* | Greece | N. Aegean Sea | 560 | F | 1.39 | 0.980 | -0.79 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | N. Aegean Sea | 384 | M | 1.27 | 0.680 | -0.27 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | N. Aegean Sea | 944 | C | 1.27 | 0.730 | -0.11 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| *Plesionika edwardsii* | Spain | Catalan Sea | 209 | F | 3.10 | 0.650 | - | 0.6902 | 3.09 | - | - | 2.90 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 239 | M | 3.20 | 0.800 | - | 0.7727 | 2.92 | - | - | 2.72 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 453 | C | 3.10 | 0.700 | - | 0.6991 | 3.07 | - | - | 2.90 | LF | EL | CL | Company & Sardá (2000) |
| | | W. Mediterranean Sea | - | F | 3.10 | 0.800 | 0.15 | 0.8387 | 2.81 | - | - | 2.91 | LF | EL | CL | García-Rodriguez *et al.* (2000) |
| | | W. Mediterranean Sea | - | M | 2.60 | 0.800 | -0.05 | 0.7900 | 2.94 | - | - | 2.88 | LF | EL | CL | García-Rodriguez *et al.* (2000) |
| *Plesionika gigliolii* | Spain | Catalan Sea | 140 | F | 2.05 | 0.750 | - | 0.9781 | 2.60 | - | - | 1.86 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 144 | M | 2.00 | 0.550 | - | 1.1562 | 2.92 | - | - | 1.60 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 285 | C | 2.10 | 0.750 | - | 0.9160 | 2.84 | - | - | 1.86 | LF | EL | CL | Company & Sardá (2000) |
| *Plesionika heterocarpus* | Greece | N. Aegean Sea | 9468 | F | 1.78 | 1.450 | -0.17 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | N. Aegean Sea | 11465 | M | 1.61 | 1.170 | -0.28 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | N. Aegean Sea | 20933 | C | 1.56 | 1.090 | -0.31 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | Spain | Catalan Sea | 129 | F | 2.30 | 0.900 | - | 0.7662 | 2.99 | - | - | 2.02 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 50 | M | 2.24 | 1.000 | - | 0.7603 | 3.09 | - | - | 1.94 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 188 | C | 2.27 | 0.900 | - | 0.7277 | 3.10 | - | - | 2.02 | LF | EL | CL | Company & Sardá (2000) |
| *Plesionika martia* | Spain | Catalan Sea | 208 | F | 3.04 | 0.390 | - | 0.6239 | 3.04 | - | - | 2.67 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 149 | M | 2.75 | 0.540 | - | 0.6059 | 3.08 | - | - | 2.39 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 370 | C | 3.01 | 0.500 | - | 0.5753 | 3.20 | - | - | 2.67 | LF | EL | CL | Company & Sardá (2000) |
| | Greece | N. Aegean Sea | 1643 | F | 2.37 | 0.710 | -0.74 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | N. Aegean Sea | 1491 | M | 2.30 | 0.580 | -0.19 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | N. Aegean Sea | 3134 | C | 2.40 | 0.730 | -0.79 | - | - | - | - | - | LF | EL | CL | Vafidis *et al.* (2004) |
| | | W. Ionian Sea | 8231 | F | 3.05 | 0.440 | - | 0.7086 | 2.85 | 1.55 | - | 2.60 | LF | EL | CL | Maiorano *et al.* (2002) |
| | | W. Ionian Sea | 6943 | M | 2.80 | 0.500 | - | 0.7230 | 2.84 | - | - | 2.50 | LF | EL | CL | Maiorano *et al.* (2002) |
| *Polycheles typhlops* | Spain | Catalan Sea | 76 | F | 4.80 | 0.350 | - | 0.1321 | 3.82 | - | - | 4.67 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 134 | M | 3.20 | 0.500 | - | 0.2435 | 3.01 | - | - | 3.00 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 210 | C | 4.95 | 0.450 | - | 0.2422 | 3.03 | - | - | 4.67 | LF | EL | CL | Company & Sardá (2000) |
| *Processa canaliculata* | Spain | Catalan Sea | 53 | F | 2.30 | 1.100 | - | 0.4624 | 3.14 | - | - | 2.00 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 90 | M | 2.10 | 0.700 | - | 0.4199 | 3.45 | - | - | 1.99 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 154 | C | 2.30 | 1.100 | - | 0.4266 | 3.37 | - | - | 2.00 | LF | EL | CL | Company & Sardá (2000) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Processa nouveli* | Spain | Catalan Sea | 24 | F | 1.35 | 1.110 | - | 0.4885 | 2.60 | - | - | 1.20 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 38 | M | 1.35 | 1.100 | - | 0.5509 | 3.24 | - | - | 1.12 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 77 | C | 1.35 | 1.100 | - | 0.5290 | 3.01 | - | - | 1.20 | LF | EL | CL | Company & Sardá (2000) |
| *Scyllarides latus* | Italy | Sicily & Linosa Islands | 59 | C | 12.72 | 0.200 | - | 0.3905 | 3.01 | - | - | - | T | EL | CL | Bianchini *et al.* (1997) |
| *Sergestes arcticus* | Spain | Catalan Sea | 35 | F | 1.65 | 0.700 | - | 0.2588 | 1.40 | - | - | 1.37 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 160 | C | 1.70 | 0.800 | - | 0.2848 | 2.31 | - | - | 1.37 | LF | EL | CL | Company & Sardá (2000) |
| *Sergia robusta* | Spain | Catalan Sea | 77 | F | 2.48 | 0.640 | - | 0.3932 | 3.03 | - | - | 2.25 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 231 | C | 2.43 | 0.640 | - | 0.3976 | 2.92 | - | - | 2.25 | LF | EL | CL | Company & Sardá (2000) |
| *Solenocera membranacea* | Spain | Catalan Sea | 1367 | F | 3.15 | 0.600 | - | - | - | - | - | 3.00 | LF | EL | CL | Demestre & Abelló (1993) |
| | | Catalan Sea | 322 | M | 2.40 | 0.500 | - | - | - | - | - | 2.10 | LF | EL | CL | Demestre & Abelló (1993) |
| | | Catalan Sea | 246 | F | 2.85 | 0.650 | - | 0.5301 | 3.38 | - | - | 2.68 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 661 | M | 2.16 | 0.560 | - | 0.5558 | 2.89 | - | - | 2.03 | LF | EL | CL | Company & Sardá (2000) |
| | | Catalan Sea | 907 | C | 2.90 | 0.650 | - | 0.5560 | 2.91 | - | - | 2.68 | LF | EL | CL | Company & Sardá (2000) |
| *Squilla mantis* | Italy | E. Ligurian Sea | - | F | 22.00 | 1.450 | - | - | - | - | - | - | - | - | TL | Righini & Baino (1996; in Piccinetti-Marfin, 1999) |
| | | E. Ligurian Sea | - | M | 22.50 | 1.300 | - | - | - | - | - | - | - | - | TL | Righini & Baino (1996; in Piccinetti-Marfin, 1999) |
| | | C. Adriatic Sea | - | F | 4.19 | 0.450 | - | 1.5351 | 3.04 | - | - | - | - | - | CL | Froglia (1996; in Maynou *et al.*, 2005) |
| | | C. Adriatic Sea | - | M | 4.12 | 0.530 | - | 1.5351 | 3.04 | - | - | - | - | - | CL | Froglia (1996; in Maynou *et al.*, 2005) |
| | Spain | Ebro Delta | 1768 | F | 20.00 | 1.300 | - | - | - | - | - | 18.00 | LF | EL | TL | Abelló & Martín (1993) |
| | | Ebro Delta | 1732 | M | 20.00 | 1.600 | - | - | - | - | - | 19.00 | LF | EL | TL | Abelló & Martín (1993) |
| **Bivalvia** | | | | | | | | | | | | | | | | |
| *Arca noae* | Croatia | Marina, E. Adriatic Sea | - | C | 3.50 | 0.160 | -0.02 | - | - | - | 13 | - | SR | NL | SHH | Peharda *et al.* (2002) |
| | | Mali Ston Gulf, E. Adriatic Sea | - | C | 3.15 | 0.170 | -0.04 | - | - | - | 16 | - | SR | NL | SHH | Peharda *et al.* (2002) |
| | | Malo Jezero, E. Adriatic Sea | - | C | 3.01 | 0.150 | -0.02 | - | - | - | 13 | - | SR | NL | SHH | Peharda *et al.* (2002) |
| *Callista chione* | Greece | Thassos Island | - | C | 6.27 | 0.240 | -0.32 | 0.1047 | 3.08 | - | - | - | SR | - | SHL | Leontarakis & Richardson (2004) |
| | | Thassos Island | - | C | 5.78 | 0.260 | -0.15 | 0.1047 | 3.08 | - | 16 | - | SR | - | SHL | Leontarakis & Richardson (2004) |
| | Italy | - | - | C | 9.04 | 0.208 | 0.14 | 0.1350 | 3.25 | - | - | - | SR | - | SHL | AA.VV. (1993; in Marano *et al.*, 1999a) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Chamelea gallina* | Italy | Adriatic Sea | - | C | 4.16 | 0.480 | -0.01 | - | - | - | - | - | SR | - | SHL | Arneri *et al.* (1995; in Marano *et al.*, 1999b) |
| | | Adriatic Sea | - | C | 4.28 | 0.790 | -0.03 | 0.3260 | 2.78 | - | - | - | - | - | SHL | Vaccarella *et al.* (1996; in Marano *et al.*, 1999b) |
| | | Tyrrhenian Sea | - | C | 3.91 | 0.500 | -0.30 | 0.4622 | 2.70 | - | - | - | - | - | SHL | Costa *et al.* (1987; in Marano *et al.*, 1999b) |
| *Donax trunculus* | Italy | E. Ligurian Sea | - | C | 3.67 | 0.500 | -0.31 | 0.1733 | 2.70 | - | - | - | - | - | SHL | Costa *et al.* (1987; in Marano *et al.*, 1999c) |
| | | S. Adriatic Sea | 31082 | C | 4.76 | 0.300 | 0.00 | - | - | 1.84 | | 3.70 | LF | EL | SHL | Zeichen *et al.* (2002) |
| | Spain | Catalan Sea | - | C | 4.18 | 0.710 | -0.35 | - | - | - | - | 3.60 | SR | NL | SHL | Ramón *et al.* (1995) |
| | France | - | - | C | 3.60 | 0.956 | 0.70 | - | - | - | - | - | LF | - | SHL | Bodoy (1982; in Ramón *et al.*, 1995) |
| *Ensis siliqua* | Italy | E. Ligurian Sea | - | C | 14.10 | 0.700 | -0.15 | 0.0096 | 3.08 | - | - | - | - | - | SHL | Costa *et al.* (1987; in Marano *et al.*, 1999d) |
| *Modiolus barbatus* | Croatia | Mali Ston Gulf | - | C | 5.98 | 0.210 | -0.10 | - | - | - | 13 | 6.55 | SR | NL | SHL | Peharda *et al.* (2006) |
| *Mytilus galloprovincialis* | Italy | C. Tyrrhenian Sea | - | C | 11.17 | 0.680 | -0.75 | - | - | - | - | 11.15 | LF | NL | SHL | Ardizzone *et al.* (1996) |
| *Paphia aurea* | Italy | Ancona | - | C | 4.47 | 0.440 | 0.37 | 0.1909 | 2.97 | 1.50 | - | 4.80 | - | - | SHL | Froglia *et al.* (1998; in Marano *et al.*, 1999$^{e}$) |
| *Pecten jacobaeus* | Croatia | Northern Adriatic Sea | 70 | C | 12.79 | 0.420 | -0.22 | - | - | - | 13 | 14.20 | SR | GH | SHL | Peharda *et al.* (2003) |
| *Pinna nobilis* | Greece | Thermaikos Gulf | 112 | C | 73.77 | 0.063 | -0.22 | - | - | - | 28 | 69.00 | SR | NL | SHL | Galinou-Mitsoudi *et al.* (2005) |
| | France | Port-Cros | - | C | 86.30 | 0.053 | 0.22 | - | - | - | 10 | - | SR | - | SHL | Moreteau & Vicente (1988) |
| | Spain | Aguamarga | - | C | 49.41 | 0.210 | -0.08 | - | - | - | 13 | - | SR | NL | SHL | Richardson *et al.* (1999) |
| | | Rodalquilar | - | C | 45.27 | 0.280 | -0.07 | - | - | - | 8 | - | SR | NL | SHL | Richardson *et al.* (1999) |
| | | Carboneras | - | C | 68.98 | 0.220 | -0.11 | - | - | - | 4 | 61.00 | SR | NL | SHL | Richardson *et al.* (1999) |
| | Croatia | S.E. Adriatic Sea | 47 | C | 72.31 | 0.160 | - | - | - | - | - | 78.00 | T | GH | SHL | Siletić & Peharda (2003) |
| *Tapes decussata* | Italy | Venice Lagoon | - | C | 5.37 | 0.440 | - | - | - | - | - | 3.98 | - | - | SHL | Breber (1985) |
| *Venus verrucosa* | Italy | Mafredonia | - | C | 5.34 | 0.280 | -1.26 | 0.1197 | 3.33 | - | - | - | - | - | SHL | Arneri *et al.* (1991; in Marano *et al.*, 1999f) |
| | | Bari | - | C | 4.28 | 0.260 | -1.34 | 0.1591 | 3.21 | - | - | - | - | - | SHL | Arneri *et al.* (1991; in Marano *et al.*, 1999f) |
| | | Genova Gulf | - | C | 5.78 | 0.157 | 1.04 | - | - | - | - | - | - | - | SHL | Vacchi *et al.* (1996; in Marano *et al.*, 1999f) |
| | | Trieste Gulf | - | C | 7.54 | 0.189 | - | - | - | - | - | - | - | - | SHL | Brizzi *et al.* (1992; in Marano *et al.*, 1999f) |
| **Cephalopoda** | | | | | | | | | | | | | | | | |
| *Loligo media* | Italy | E. Ligurian Sea | - | F | 10.58 | 0.200 | - | - | - | 6.00 | - | - | LF | - | ML | Auteri *et al.* (1987; in Belcari, 1999) |
| | | E. Ligurian Sea | - | M | 7.94 | 0.270 | - | - | - | 5.00 | - | - | LF | - | ML | Auteri *et al.* (1987; in Belcari, 1999) |

**Table A1.** Continued.

| Species | Country | Locality | N | S | $L_\infty$ | $K$ | $t_0$ | $a$ | $b$ | $L_m$ | $T_{max}$ | $L_{max}$ | AM | M | LT | Reference I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Eledone cirrhosa* | Italy | Ligurian Sea | 217 | F | 19.28 | 0.387 | -0.03 | - | - | - | - | 15.50 | LF | EL | ML | Orsi Relini *et al.* (2006) |
| | | Ligurian Sea | 202 | M | 15.56 | 0.422 | -0.07 | - | - | - | - | - | LF | EL | ML | Orsi Relini *et al.* (2006) |
| *Illex coindetii* | Spain | Catalan Sea | 416 | F | 29.27 | 0.205 | - | - | - | - | - | 24.00 | LF | FW | ML | Sánchez (1984) |
| | | Catalan Sea | 371 | M | 25.67 | 0.202 | - | - | - | - | - | 18.00 | LF | FW | ML | Sánchez (1984) |
| *Octopus vulgaris* | Spain | - | - | C | 30.00 | 0.720 | - | - | - | - | - | - | - | - | ML | Guerra (1979; in Belcari & Sartor, 1999) |
| | Tunisia | Gabes Gulf | - | C | 29.60 | 0.560 | -0.23 | - | - | 14.50 | - | - | LF | - | ML | Zguidi (2002; in Ezzeddine & El Abed, 2004) |
| *Sepia officinalis* | Tunisia | Tunisian coasts | - | F | 27.06 | 0.831 | -0.05 | - | - | - | - | 26.00 | LF | EL | ML | Ezzeddine-Najai & El Abed (2001) |
| | | Tunisian coasts | - | M | 29.51 | 0.723 | -0.06 | - | - | - | - | 27.00 | LF | EL | ML | Ezzeddine-Najai & El Abed (2001) |
| | | Tunisian coasts | 2459 | C | 28.58 | 0.739 | -0.07 | - | - | - | - | 27.00 | LF | EL | ML | Ezzeddine-Najai & El Abed (2001) |
| **Holothuroidea** | | | | | | | | | | | | | | | | |
| *Holothuria polii* | Algeria | Sidi-Fredj | 15 | C | 18.72 | 0.690 | - | - | - | - | - | 16.50 | LF | EL | VL | Mezali & Semroud (1998) |
| *Holothuria sanctori* | Algeria | Sidi-Fredj | 10 | C | 16.10 | 0.250 | - | - | - | - | - | 16.50 | LF | EL | VL | Mezali & Semroud (1998) |
| *Holothuria tubulosa* | Algeria | Sidi-Fredj | 26 | C | 14.34 | 0.660 | - | - | - | - | - | 13.15 | LF | EL | VL | Mezali & Semroud (1998) |
| **Anthozoa** | | | | | | | | | | | | | | | | |
| *Corallium rubrum* | - | - | - | C | 35.00 | 0.060 | - | - | - | - | - | - | - | - | - | Garcia (1984; in Campisi & Murenu, 1999) |

# GROWTH ESTIMATES OF THE SPINY LOBSTER, *PANULIRUS LONGIPES* IN CAPTIVITY[1]

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## ABSTRACT

Growth determination studies were conducted on spiny lobsters, *Panulirus longipes* (A. Milne-Edwards, 1868) in captivity to determine their growth rates and to estimate von Bertalanffy growth parameters, i.e., asymptotic carapace length ($L_\infty$) and the growth constant ($K$) using the Gulland and Holt method.

Molting frequency in smaller individuals was higher than in larger animals. The mean single molt increments of lobsters (2.0-4.9 cm) ranged from 0.2 to 0.27 cm carapace length and 6.1 to 15.0 g total weight, with mean intermolt days of 32.5 to 60.1 days. Mean intermolt days of group-reared lobsters (4.0-4.9 cm) were significantly higher ($P<5\%$) than for smaller lobsters (2.0-3.9 cm), both group- and individually-reared. Spiny lobsters which were reared in captivity had an estimated asymptotic carapace length of 6.9 cm and 7.6 cm and $K$ of 0.68 year$^{-1}$ and 0.51 year$^{-1}$ for group- and individually-reared lobsters, respectively.

## INTRODUCTION

Knowledge of growth is essential to the basic understanding of the biology of any organism and may provide useful information both for culture and resource management considerations of commercially important species, such as spiny lobsters. Although extensive studies have been conducted on the Western Australian spiny lobster (*Panulirus cygnus* George, 1962), little is known about its counterpart in the Philippines, *Panulirus longipes* (A. Milne-Edwards, 1868).

This study, conducted from January to December 1987, investigated the growth of the spiny lobster *P. longipes* in captivity in order to obtain estimates of the von Bertalanffy growth parameters, asymptotic carapace length ($L_\infty$) and growth constant ($K$), as part of a larger study on their biology and ecology (Garces, 1988).

## MATERIALS AND METHODS

### *Acquisition of experimental animals*

Live *P. longipes* were bought from fishermen in Bolinao, Pangasinan, Philippines, who collected them in the coral reef areas off the coast of Balingasay (Figure 1). These lobsters inhabit reef flats or areas deeper down the seaward portion of the outer reef.

### *Growth determination*

The lobsters were held in a compartmentalized wooden tank (2.4 x 1.2 x 0.9 m), i.e., within individual stocking compartments (0.4 x 0.3 x 0.9 m) and group stocking compartments (0.6 x 0.5 x 0.9 m). Stocking density was approximately 10 lobsters·m$^{-2}$. Hollow blocks were provided as shelters to simulate natural crevices. The experimental setup was provided with flow-through sea water at a rate of 2.3 l·min$^{-1}$ during daytime when the pumps are running with twenty hour aeration. Every afternoon, lobsters were fed *ad libitum* with clams (Family Veneridae) and/or gastropods (*Strombus* sp.). Excess food was removed every morning to prevent fouling.

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Carapace length (CL), total weight (TW) and sex of each lobster were determined prior to growth studies. The lobsters were tagged with colored wires tied to the base of an antenna to ensure accurate monitoring of an individual's growth.

The date of each molt was recorded and the respective CL and TW were measured after 3 days when the new shell had hardened. Newly-molted lobsters were then retagged. All molting incidences were treated as single molts and grouped into 1-cm size classes. First molts in captivity and succeeding molts (i.e., second and third molts) were treated separately because part of the inter-molt period prior to the first molt in captivity was spent in the wild. This was done to eliminate the probable differences in the growth increments (Chittleborough, 1975).

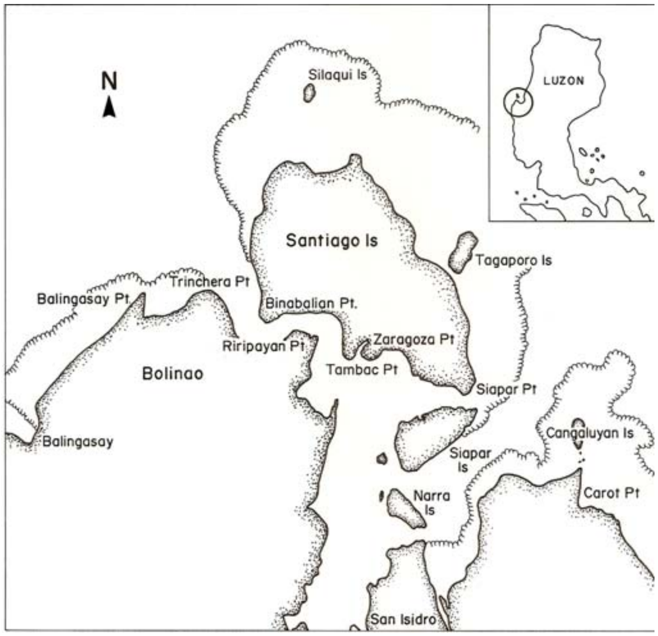

**Figure 1.** Map of study area in Bolinao, Pangasina, Philippines.

### *Growth Parameter Estimates*

A Gulland and Holt Plot (Pauly, 1984) was used to estimate the asymptotic length ($L_\infty$) and the growth constant ($K$) of *P. longipes longipes*. A plot of size increments per unit time against mean size (for the increment in question) gives a straight line whose slope is an estimate of the value of K.

### *Statistical Analysis*

Growth data such as CL increments and intermolt days were tested using unbalanced 2-way nested ANOVA. This was done to determine the differences in growth performance among the size groups and between individually and group-reared lobsters per size class. Multiple mean comparisons were also done.

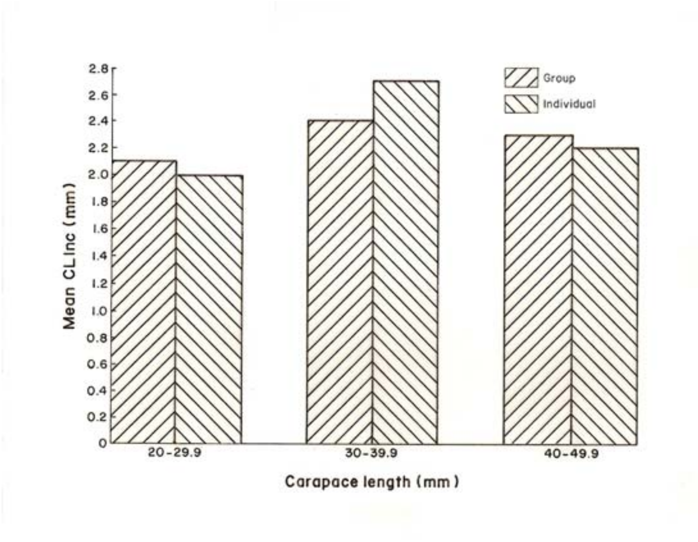

**Figure 2.** Mean carapace length increment per molt per size class of *Panulirus longipes* reared in experimental tanks at the Bolinao Marine Laboratory, University of the Philippines - Marine Science Institute at Bolinao, Pangasinan, Philippines.

## RESULTS

Of the 54 *P. longipes* reared in captivity at the Bolinao Marine Laboratory, 20 were reared individually, while 34 were reared in groups. The mean carapace length increment ($CL_{Inc}$) increased with size with 3.0-3.9 cm CL size class exhibiting the highest increments (Table 1, Figure 2). In terms of total weight increment ($TW_{Inc}$), larger individuals had greater $TW_{Inc}$ than smaller animals (Figure 3). Similarly, mean intermolt days (IntD) increased with increasing size, while the percentages of $CL_{Inc}$ and $TW_{Inc}$ decreased with increase in size.

Figure 3 shows that the total weight increments of individuals held in isolation were higher than those held in groups. However, those in groups had higher $CL_{Inc}$ except those in size class 3.0-3.9 cm CL (Figure 2). Moreover, lobsters held in groups exhibited shorter mean IntD than individually held animals, except those in size class 4.0-4.9 cm CL (Table 1).

**Table 1.** Differences in growth based on single molts for the succeeding molt per size class for individually and group-reared spiny lobsters *Panulirus longipes* from tank experiments at the Bolinao Marine Laboratory, University of the Philippines - Marine Science Institute at Bolinao, Pangasinan, Philippines. Standard deviations of size increments and intermolt days are in brackets.

| Treatment | Class size (cm) | Sample size | Mean Length (CL, cm) | Length increments (CL, cm) | Mean Weight (TW, g) | Weight increments (TW, g) | Number of molts | Mean intermolt days |
|---|---|---|---|---|---|---|---|---|
| Indiv. | 2.0-2.9 | 5 | 2.6 | 0.20 (0.24) | 22.3 | 6.8 (6.5) | 11 | 38.4 (6.7) |
| Grouped | | 11 | 2.5 | 0.21 (0.29) | 17.9 | 6.1 (7.2) | 14 | 32.6 (7.6) |
| Indiv. | 3.0-3.9 | 4 | 3.5 | 0.27 (0.23) | 45.0 | 13.8 (5.0) | 4 | 49.0 (12.4) |
| Grouped | | 7 | 3.6 | 0.24 (0.41) | 53.6 | 10.0 (18.3) | 7 | 45.3 (8.8) |
| Indiv. | 4.0-4.9 | 7 | 4.4 | 0.22 (0.20) | 88.5 | 15.0 (11.2) | 10 | 58.8 (10.5) |
| Grouped | | 11 | 4.6 | 0.23 (0.24) | 117.0 | 14.0 (19.5) | 15 | 60.1 (16.3) |

Although carapace length increments did not differ significantly between individually and group-reared lobsters and among size classes, mean intermolt days of group reared lobsters with size 4.0-4.9 cm CL were significantly higher ($P < 5\%$) than those of smaller lobsters (2.0-3.9 cm CL). Mean intermolt days of group and individually reared lobsters of the same size class were not significantly different (Table 1).

**Table 2.** Growth parameters etimated via the Gulland and Holt Plot for *Panulirus longipes* reared in experimental tanks at the Bolinao Marine Laboratory, University of the Philippines - Marine Science Institute at Bolinao, Pangasinan, Philippines

| Stocking | $L_\infty$ (CL, cm) | $K$ | r | Sample size | Length range (CL, cm) |
|---|---|---|---|---|---|
| Group | 6.88 | 0.68 | -0.8958 | 19 | 2.02-5.72 |
| Individual | 7.56 | 0.51 | -0.8631 | 7 | 2.63-4.72 |

Preliminary growth estimates for *P. longipes* from the Gulland and Holt Plot are presented in Table 2. Individually reared lobsters attained higher asymptotic length ($L_\infty$) values (7.6 cm) than those held in groups (6.9 cm). In contrast, those in groups had higher $K$ values than individually reared lobsters at 0.68 $\text{year}^{-1}$ and 0.51 $\text{year}^{-1}$, respectively (Figures 4a and 4b). This may suggest that group reared animals grow faster than those held in isolation.

# DISCUSSION

Growth of *P. longipes,* as in other decapod crustaceans took place discontinuously in a series of steps when ecdysis occurs. Therefore, growth is determined by the increase in CL and TW as well as molting frequency. Growth rates of *P. longipes* were highest in smaller individuals and decreased with increasing size. This finding is comparable with results of similar studies on *P. argus* (Travis, 1954) and *Jasus lalandii* (Fielder, 1964). Similar conclusions were also derived by Berry (1971) for *P. homarus* and Gomez & Junio (1985) for *P. ornatus*, *P. versicolor* and *P. longipes* based on carapace length increments and molting frequency. Decreasing growth rates in larger animals may be more influenced by increasing intermolt periods with size rather than smaller carapace length or total weight increments.

The mean single molt increment of *P. longipes* (2.0-4.9 cm CL) ranged from 0.20-0.27 cm CL and 6.1-15.0 g TW, with mean intermolt days of 32.5-60.1 (Table 1). This is comparable with results obtained by Gomez & Juinio (1985) using the same species wherein the average single molt increment was 0.17 cm for CL ranging from 5.52-6.44 cm, and an average of 80 intermolt days (or 4.55 $\text{molts}\cdot\text{year}^{-1}$).

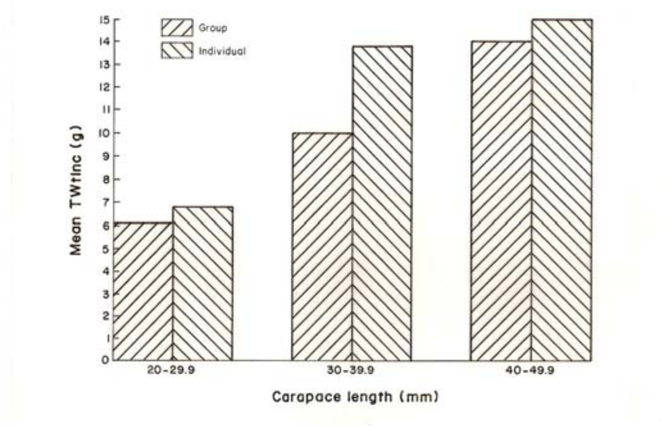

**Figure 3.** Mean total weight increment per molt per size class of *Panulirus longipes* reared in experimental tanks at the Bolinao Marine Laboratory, University of the Philippines - Marine Science Institute at Bolinao, Pangasinan, Philippines.

The slight decrease in carapace length increments of the lobsters at 4.0-4.9 cm CL suggests that the growth rate may be slightly depressed as they reach sexual maturity (Figure 3). As observed by Travis (1954) in his work on *P. argus*, the growth rate of juveniles was rapid and decreased as they approached sexual maturity. Moreover, Berry (1971) pointed out that a decline in CL increment was observed at 5.0 cm CL in *P. homarus*, the size at sexual maturity. Similarly, Gomez & Juinio (1985) reported that the smallest egg-bearing female *P. longipes* is 4.18 cm CL. Therefore, the size at first sexual maturity for *P. longipes* may be about 4.0 cm CL.

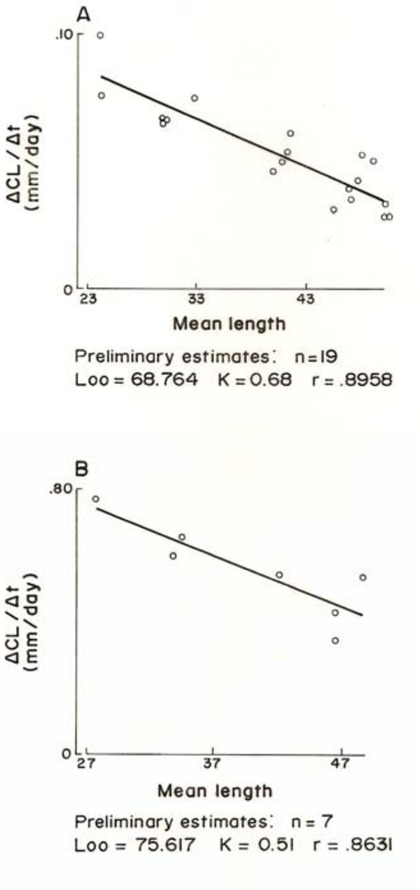

**Figure 4**. Growth estimates of *Panulirus longipes* (pooled both sexes) from the Gulland and Holt Plot. A: Group stocking. B: Individual stocking.

**Table 3**. Growth parameters and growth performance indices (Φ'= log10K +2log10L from Pauly & Munro 1984) of three species of *Panulirus* from five different localities. Note clear morphological differences between the generally larger males and the smaller females.

| Species | Sex | Location | $L_\infty$ (cm) | $K$ $(\text{year}^{-1})$ | Φ′ | Source; Remarks |
|---|---|---|---|---|---|---|
| *P. homarus* | M | Durban, S. Africa | 12.0 | 0.177 | 3.406 | Smale (1978) |
| | F | Durban, S. Africa | 9.42 | 0.337 | 3.476 | Smale (1978) |
| *P. longipes* | both | Aquaria/Australia | 11.3 | 0.459 | 3.768 | Chittleborough (1976) |
| *P. longipes* | both | Bolinao, Pangasinan | 8.8 | 0.379 | 3.469 | This study; lobsters reared in groups |
| *P. longipes* | both | Philippines | 13.4 | 0.181 | 3.511 | This study; lobsters reared individually |
| *P. penicillatus* | M | Enewetok Atoll, | 14.6 | 0.211 | 3.653 | Ebert and Ford (1986) |
| | F | Marshall Islands | 9.65 | 0.580 | 3.732 | Ebert and Ford (1986) |
| *P. penicillatus* | M | Sta. Ana, Cagayan, Philippines | 16.1 | 0.131 | 3.530 | Arellano (1989) ; K is estimated from Φ′, based on two other values for male lobsters |
| | F | | 15.3 | 0.172 | 3.604 | Arellano (1989) ; K is estimated from Φ′, based on two other values of female lobsters |

Growth increments per molt of *P. longipes* were apparently not affected by crowding since food supply was in excess. Also those lobsters held in groups had higher growth rates than those held in isolation. This observation is similar with results of earlier studies on *P. cygnus* in Western Australia, where Chittleborough (1975) reported that individually reared juveniles grew less than when they were held in groups. In addition, laboratory and field studies (Chittleborough 1976) showed that limited food supply is the primary cause of retarded growth.

Finally, results obtained from this study also indicate that the growth parameter estimates for *P. longipes* are comparable with those of other species (Table 3).

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# DEVELOPMENT AND GROWTH OF EDIBLE OYSTERS (OSTREIDAE) IN PAPUA NEW GUINEA[1]

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## ABSTRACT

This study is based on hitherto-unpublished field and laboratory work conducted by the first author in the early 1970s, but still considered useful; the second author provided updates and a more recent context.

Larval development rates to the trochophore stage of the Papua New Guinea oysters *Crassostrea amasa* (Iredale) and ecomorphs of *C. echinata* (Quoy & Gaimard) are compared in different thermohaline regimes. The conspecificity of these ecomorphs is reflected in the similar thermohaline conditions that produce optimum development rates. Embryos of the *C. echinata* ecomorphs appear to prefer warmer less saline waters than *C. amasa*, the latter preferring almost oceanic conditions. These differences are reflected in the respective habitats of adult oysters.

At least eight oyster species occur around the Papua New Guinea coastline. Three rock oysters (*Crassostrea* spp.) were studied with respect to their farming potential. The mangrove oyster (*C. echinata*) appeared suitable by its size and excellent condition attained, but the period of good condition was not predictable and collectors failed to attract spat. The Pacific oyster *C. gigas*, may be considered for introduction as a mariculture species, as it has been successfully introduced and farmed in other countries, but the high temperature would likely hinder reproduction and settlement, and seedlings would have to be imported for each new generation.

## INTRODUCTION

In the 1980s, attempts to establish farms on the Papuan coast, in Milne Bay, Galley Reach and Yule Island, of native Papua New Guinea oysters, e.g., *Saccostrea cucullata* (Born, 1778), were unsuccessful. Water temperatures or salinities were believed to be the cause of these failed experiments. Observations in Port Moresby harbor in 1972 and 1973 showed that oysters were spawning throughout most of the year in both hyper and hyposaline conditions. Peaks in settlement suggested that larval development was more successful in certain combinations of salinity and temperature than others. Previous work indicated ranges of these parameters experienced by oysters *in vivo*, which is information useful in aquaculture. However, available information on these projects, in Department of Agriculture, Stock and Fisheries files, is inadequate to assess the potential of the native oysters for farming.

The work described in this paper includes unpublished experiments of the first author, who examined some aspects of oyster biology relevant to farming, including seasonality of settlement and condition factor of local species in the Port Moresby area. A series of experiments carried out in 1973 to determine the rate of development and success of larval cultures of these oysters at various salinities and

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temperatures is presented and discussed. In addition, the growth of members of the Family Ostreidae is compared with the widely-used mariculture species, the Pacific oyster, *Crassostrea gigas* (Thunberg, 1793), and the wisdom of a possible introduction of this species for mariculture is discussed.

### *Species*

The Papua New Guinea coastline provides habitats for a number of species of edible oysters belonging to the Family Ostreidae. In the study done by the first author in the 1970s, he found that sub-littoral isolated individuals of *Pycnodonte hyotis* (Linnaeus, 1758), *Ostrea folium* Linnaeus, 1758 and *Ostrea trapezina* Lamarck, 1819 were common. A small intertidal *Ostrea* sp. forms clusters but it is too small (1.5 cm diameter) for culture purposes. There are several rock oysters (*Crassostrea* spp.) which could be considered for farming, occurring around most of the mainland and outer islands. Two are clustering species, forming dense discrete intertidal zones in harbours and bays, the black lip, *Crassostrea echinata* and *C. amasa*, the milky oyster. The third occurs as large individuals on mangrove roots or stones and is known locally as the mangrove oyster. It has also been identified as *C. echinata*. In Lombrum harbour, Manus Island, very large isolated individuals of *C. tuberculata* occur. The specific and generic classification of Indo-Pacific oysters is controversial, and the three *Crassostrea* species may in fact be sub-species of *Saccostrea cuccullata*, i.e., *S. c. echinata*, *S. c. camasa* and *S. c. tuberculata* (P. Dinamani, pers. comm. to J. Maclean).

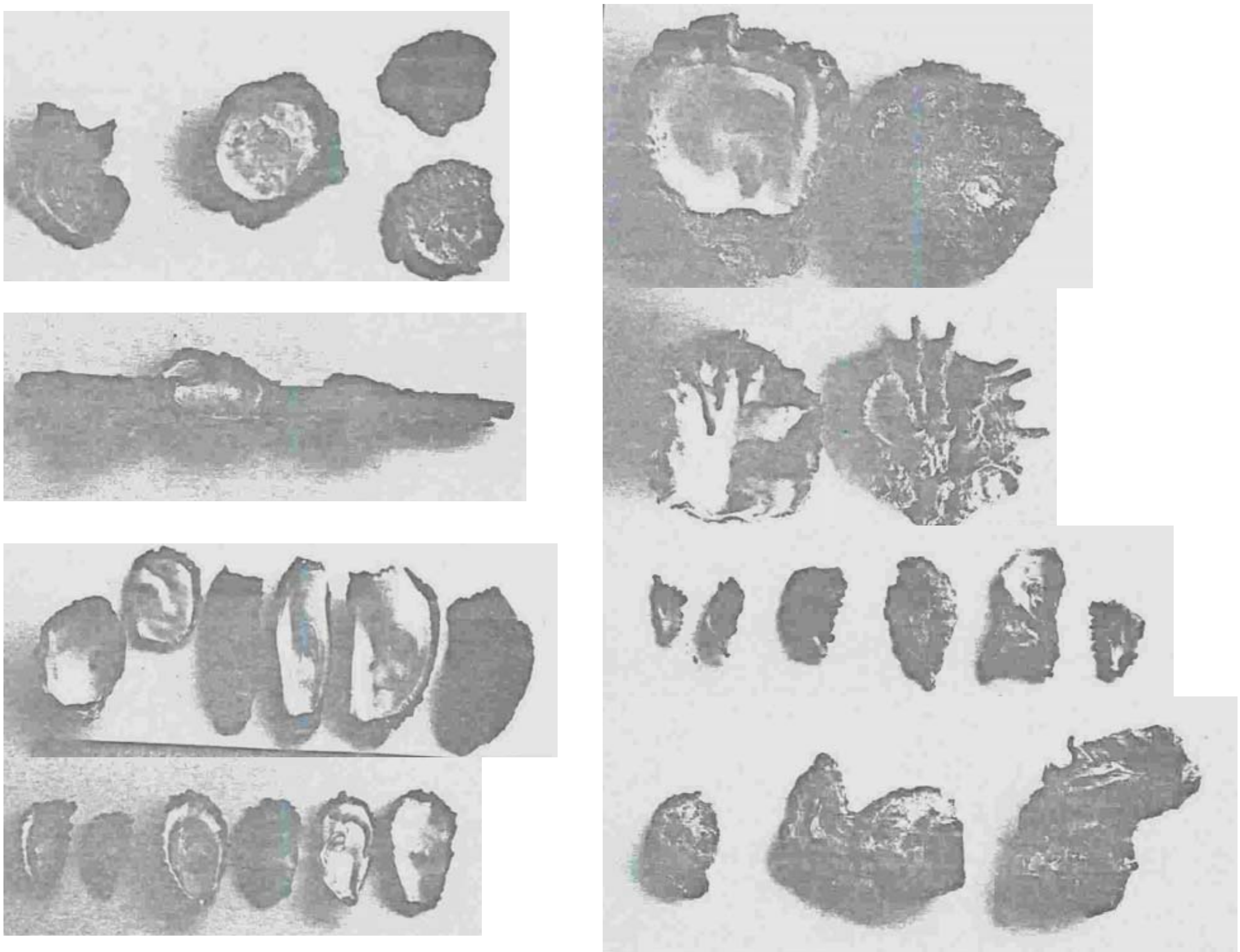

**Figure 1**. Species of Ostreidae occurring in Papua New Guinea. Left panel, top to bottom: *Crassostrea echinata* from Port Moresby harbour wharf piles; Port Moresby harbour mangroves; Bootless Bay and Fairfax harbours mangroves. Right panel, top to bottom: *Pycnodonte hyotis* (Port Moresby harbour); *Ostrea trapezina* (Port Moresby harbour); and different forms of *C. amasa* (Port Moresby harbour).

### *Habitat*

The three oyster varieties considered for farming studies had different habitats. *C. amasa* preferred stone surfaces on more exposed areas, (west and outer Port Moresby harbour) *C. echinata* preferred vertical structures in sheltered areas (wharf area of Port Moresby Harbour), while the mangrove oyster appeared to favour exposed areas with a fast current, on stones and mangroves (Bootless Bay reef shallows).

### *Size*

Only one species, the mangrove oyster, attains a commercially acceptable size in natural conditions for 'in shell" sale. Table 1 shows the average sizes of 120 individuals of each of the three species. *C. echinata* was always flat (Figure 1) and thin shelled, indicating rapid growth. The other two species were well cupped and of thicker shell suggesting slower growth rate.

**Table 1**. Average volume of 120 oysters in cm³.

| Species | Whole | Shells | Meat |
|---|---|---|---|
| Black lip | 9.0 | 6.2 | 1.8 |
| Milky | 9.2 | o.5 | 1.3 |
| Mangrove | 43.0 | 34.4 | 6.6 |

## MATERIALS AND METHODS

### *Larval cultures*

Gonad material was removed from adult oysters by small spatula. Eggs were sieved through a series of collars of different mesh size to remove gross foreign matter, placed in Petri dishes of filtered seawater of selected salinity and washed in similar water by pipette. A small quantity of sperm was added, and where there was foreign matter in the sperm or an excess of it, the eggs were washed again after a few minutes.

Dishes and containers of seawater had previously been placed in a water bath held at the desired temperature. Temperature accuracy was to ±0.1°C. Temperatures chosen were 25, 27.5, 30, 32.5 and 35°C. Salinities were dilutions of normal seawater by distilled water from 100% seawater, 80 %, 60 % to 40 % seawater. For *C. amasa*, 70 % seawater was also used.

After fertilization the eggs were inspected every five minutes in the order that sperm was added; times of first occurrence of polar bodies, cell divisions and finally movement of the larvae were recorded. Duplicate dishes were always used.

Onset of movement of the trochophore was the last stage measured. Larvae generally failed to reach the next, D shaped veliger stage. The few that did survive would not accept available food, sterile mono-specific cultures of *Chlorella pyrenoidosa* and *Dunaliella tertiolecta*. The algae[3] were maintained in media and conditions as described by Loosanoff & Davis (1963). Success of cultures was measured by fertilization rate and numbers of abnormal larvae[4].

**Figure 2**. Asbestos cement spat collector used in Port Moresby harbour consisting of 12 plates, each 48" x 3" set 0.5" apart. The plates are supported by a steel frame and the whole collector suspended by ropes below a jetty. A free standing version on shore was abandoned due to vandalism.

### *Seasonality of settlement*

To determine settlement periods of the oysters, intertidal spat collectors were placed in representative areas in Fort Moresby Harbor and Bootless Bay. For *C. amasa*, bunks of fibro collectors (Figure 2) (Thomson, 1950) were set out near Napa Napa. However, after three successive collectors were vandalized, this site was abandoned. For *C. echinata*, similar fibro collectors were hung below the Navy wharf in the harbor from March 1972 to October 1973. Results are shown in Table 2.

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[3] Starter cultures from Commonwealth Scientific and Industrial Research Organization (CSIRO) Marine Biochemistry Section, Sydney. *Isochrysis* and *Monochrysis* cultures were also supplied but died, presumably through temperature stress.

[4] While no laboratory cultures of oysters passed the D stage veliger, one culture did produce a light spatfall on fibro plates in an outdoor concrete tank 2 x 1 x 1 m. Larvae were added to the tank at the trochophore stage into filtered seawater enriched with the *Chlorella* and *Dunaliella* cultures, though not in sufficient quantity to tint the water (about 10,000 c.c.-1). Salinity was approximately 29‰ and temperature range 25 to 27.5°C. Since this experiment was preceded by a number of unsuccessful ones, settlement was not monitored daily. Spat were first observed on the 14th day from fertilisation, when they were perhaps two days old. The larval period at these temperatures was then about 12-13 days. Settlement would undoubtedly have occurred in less time in warmer water.

Table 2 shows there was a major spat fall within the period March-May 1972, and minor spatfalls from November to April, 1973. Outside these periods there was virtually no settlement.

In the case of mangrove oysters, cement bricks were set out in the adult habitat in Bootless Bay from November 1972 to November 1973. No settlement was recorded during this period. Empty shells held in netting bags were set out from May to November, 1973, but these also failed to attract spat.

**Table 2.** Spat settlement of black-lipped oyster, *Crassostrea echinata*, on fibro collector plates, Port Moresby harbour.

| Period submerged | Upper surface | Lower surface | Remarks |
|---|---|---|---|
| Mar 2-28 1972 | - | - | medium barnacle growth |
| Mar 28 - May 15 | 119.0 | 86.0 | heavy barnacle, and *Pinctada* settlement; medium sea squirts, mainly on lower plates. |
| Jun 9 - Jul 6 | - | - | light algal covering |
| Jul 6 - Sep 7 | 0.2 | 1.5 | heavy barnacle settlement |
| Sep 5 - Oct 1 | - | - | - |
| Oct 1 - Nov 10 | 0.0 | 2.0 | - |
| Nov 10 - Feb 2 1973 | 16.3 | 27.5 | heavy sea squirt settlement |
| Feb 23 - Apr 19 | 5.8 | 32.9 | plates fairly clean, few barnacles or sea squirts |
| Apr 19 - Jun 4 | - | - | - |
| Jun 4 - Jul 12 | - | - | fairly clean |
| Jul 12 - Sep 5 | - | 0.4 | - |
| Sep 6 - Oct 16 | 0.3 | 3.0 | clean to very light algae |

### *Seasonality of spawning*

Gonad smears of the three varieties of oysters were examined microscopically each month to determine sex and gonad stage. In practice, it was possible to detect three states of gonad development only: ripe, spending and spent or immature. Ripe oysters had full gonads, in which eggs or sperm were clearly distinguishable; spending oysters were semi-flaccid, not full, but still contained recognizable eggs and spermatozoa. Spent oysters contained very small gonads in most of which were very few eggs or

**Table 3**. Gonad analysis of three species of *Crassostrea* from Port Moresby, Papua New Guinea.

| Species | Year | Month | No. | Sex ratio | Ripe | Females Spending | Spent | Ripe | Males Spending | Spent |
|---|---|---|---|---|---|---|---|---|---|---|
| *C. amasa* | 1972 | June | 84 | 0.20 | 43 | 10 | 13 | 12 | - | 5 |
| (Milky oyster) | | July | 20 | 0.40 | 9 | 2 | 1 | 5 | 3 | - |
| | | September | 30 | 0.16 | 5 | 15 | 5 | - | 5 | - |
| | | October | 30 | 0.07 | 2 | 22 | 4 | - | 2 | - |
| | | December | 30 | 0.20 | 2 | 10 | 12 | - | 6 | - |
| | 1973 | January | 30 | 0.67 | 1 | 3 | 6 | 1 | 11 | 8 |
| | | February | 60 | 0.33 | - | 24 | 16 | - | 20 | - |
| | | June | 30 | 0.27 | 5 | 11 | 6 | - | 8 | - |
| | | September | 30 | 0.17 | - | 20 | 5 | - | 5 | - |
| | | October | 30 | 0.37 | - | 13 | 6 | - | 11 | - |
| *C. echinata* | 1972 | June | 41 | 0.29 | 9 | 5 | 15 | 6 | 1 | 5 |
| (Black lip oyster) | | July | 20 | 0.60 | 3 | 5 | - | 6 | 6 | - |
| | | August | 47 | 0.26 | 13 | 15 | 8 | 5 | 6 | 1 |
| | | September | 30 | 0.27 | 4 | 12 | 6 | - | 8 | - |
| | | October | 49 | 0.16 | 6 | 35 | - | - | 8 | - |
| | | November | 22 | 0.14 | - | 15 | 4 | - | 3 | - |
| | | December | 30 | 0.47 | 5 | 8 | 3 | - | 14 | - |
| | 1973 | February | 30 | 0.37 | - | 11 | 8 | - | 11 | - |
| | | March | 22 | 0.14 | - | 15 | 3 | - | 3 | - |
| | | April | 30 | 0.27 | - | 14 | 8 | - | 8 | - |
| | | May | 30 | 0.23 | 4 | 14 | 5 | - | 7 | - |
| | | June | 30 | 0.17 | - | 18 | 7 | - | 5 | - |
| | | July | 60 | 0.35 | 2 | 31 | 6 | - | 21 | - |
| | | September | 30 | 0.53 | - | 12 | 2 | - | 16 | - |
| *C. echinata* | 1972 | November | 30 | 0.47 | - | 16 | - | - | 14 | - |
| (Mangrove oyster) | | December | 30 | 0.37 | 4 | 15 | - | - | 11 | - |
| | 1973 | January | 30 | 0.53 | - | 11 | 3 | - | 16 | - |
| | | February | 30 | 0.23 | 2 | 20 | 1 | - | 5 | 2 |
| | | March | 18 | 0.56 | 1 | 4 | 3 | - | 10 | - |
| | | April | 30 | 0.26 | - | 21 | 1 | - | 8 | - |
| | | June | 30 | 0.37 | - | 12 | 7 | - | 11 | - |
| | | July | 30 | 0.43 | - | 12 | 5 | - | 13 | - |
| | | August | 30 | 0.40 | 2 | 14 | - | - | 12 | - |
| | | September | 30 | 0.53 | - | 4 | 10 | - | 16 | - |
| | | October | 30 | 0.57 | - | 9 | 4 | - | 17 | - |
| | | November | 30 | 0.37 | - | 19 | - | - | 11 | - |

spermatozoa. Females contained mainly small oocytes, while males contained spermatocytes.

Interestingly, it was only when gonad material was virtually indistinguishable that no viable eggs were present. In all months of the year, viable sperm could be obtained and eggs fertilized from specimens of all three species.

The results of gonad analysis are shown in Table 3. In *C. amasa*, significant proportions of ripe males and females were present in two months only, June and July, 1972. In all other months sampled, most individuals were spending. *C. echinata* males were ripe from June to August, 1972, although some females remained so until November. In the majority of sampled months, most individuals were spending. The same was true of the mangrove oyster. In this species, no ripe males and few ripe females were found.

In all three species, the sex ratio varied considerably from month to month, without obvious pattern.

*Condition*

Oysters were easily obtainable as intact specimens from their substrate and initially condition was determined each month in terms of volume of meat as a percentage of whole volume. Later, condition was also measured in terms of volume of meat as a percentage of shell space (whole volume minus volume of valves). Thirty oysters were used for each determination. Meats were drained and volumes found by displacement of water.

Condition factors by month are shown in Table 4. Condition as a factor of whole volume varied erratically from month to month indicating wide variation in relative volume of shells between individuals.

**Table 4**. Condition factors, i.e., volume of meat (M) as a ratio of the volume of the whole animal (W) and of shell space (S), of edible oysters from the Port Moresby area in 1972-73. Each sample comprises 30 specimens.

| Species | Year | Month | M/W (% vol.) | M/S (% vol. |
|---|---|---|---|---|
| *Crassostrea amasa* | 1972 | February | 12.2 | - |
| (Milky oyster) | | March | 8.1 | - |
| | | April | 11.6 | - |
| | | May | 8.3 | - |
| | | June | 8.2 | - |
| | | July | 8.4 | - |
| | | August | 14.6 | - |
| | | September | 16.5 | - |
| | | October | 10.5 | - |
| | | November | 15.2 | 80.6 |
| | | December | 20.1 | 62.1 |
| | 1973 | January | 11.7 | 50.0 |
| | | February | 16.5 | 53.2 |
| | | June | 11.7 | 60.6 |
| | | September | 14.0 | 100.0 |
| | | October | 6.7 | 33.0 |
| *C. echinata* | 1972 | February | 19.0 | - |
| (Black lip oyster) | | March | 13.0 | - |
| | | April | 14.4 | - |
| | | June | 23.6 | - |
| | | July | 6.3 | - |
| | | August | 14.3 | - |
| | | September | 19.7 | - |
| | | October | 11.8 | - |
| | | November | 18.6 | 57.9 |
| | | December | 5.3 | 26.5 |
| | 1973 | January | 12.8 | 42.2 |
| | | February | 23.7 | 49.0 |
| | | March | 25.0 | 55.6 |
| | | April | 15.7 | 58.0 |
| | | April bis | 26.8 | 80.0 |
| | | May | 24.7 | 53.7 |
| | | June | 20.4 | 71.8 |
| | | July | 13.7 | 75.5 |
| | | July bis | 14.5 | 55.6 |
| | | September | 19.6 | 69.2 |
| *C. echinata* | 1972 | October | 25.0 | 99.6 |
| (Mangrove oyster) | | December | 21.8 | 100.0 |
| | 1973 | January | 27.0 | 89.1 |
| | | February | 15.2 | 95.2 |
| | | April | 23.3 | 96.8 |
| | | June | 13.0 | 57.8 |
| | | July | 14.7 | 95.4 |
| | | August | 20.2 | 74.8 |
| | | September | 9.7 | 54.4 |
| | | October | 16.5 | 66.3 |
| | | November | 15.6 | 69.0 |

The number of determinations of condition as a factor of shell space was insufficient to show any cyclic patterns. Black lip oysters never attained “good” condition (say over 90% full) in sampled months but there appeared to be a tendency for better condition in the latter part of the year. Even where two samples were taken in the same month (April and July 1973), condition had changed significantly. Milky oysters were full on one sampling occasion only. Mangrove oysters on the other hand exhibited good condition from October 1972 to March 1973 and in July 1973. However in October and November 1973 their condition was relatively poor.

*Larval sampling*

Near surface phytoplankton hauls were made fortnightly using a 48 micron net at a station in Port Moresby harbor, May 1972-October 1973, to estimate relative abundance of bivalve larvae. The number of larvae in the samples was always very low and no seasonal variation was detected. Sub-samples were analyzed by Drs. Dinamani and Booth, New Zealand taxonomists, who found possible ostriids in one haul only, 9 August, 1973. Evidently, the sampling method was inadequate to monitor oyster spawning in this situation.

**Table 5**. Average monthly water temperature, salinity and rainfall in the Port Moresby area.

| Year | Month | Water temp. (°C) | Salinity (‰) | Rainfall (mm) |
|---|---|---|---|---|
| 1972 | May | 27.8 | - | 133 |
| | June | 27.0 | - | 5 |
| | July | 25.9 | 38.0 | 8 |
| | August | 25.3 | 37.7 | 0 |
| | September | 24.9 | 37.5 | 0 |
| | October | 26.4 | 36.8 | 5 |
| | November | 27.9 | 36.6 | 2 |
| | December | 28.8 | 37.0 | 2 |
| 1973 | January | 30.3 | 36.1 | 236 |
| | February | 29.7 | 34.7 | 103 |
| | March | 30.4 | 32.9 | 216 |
| | April | 30.0 | 33.7 | 37 |
| | May | 28.6 | 35.6 | 150 |
| | June | 28.4 | 36.0 | 56 |
| | July | 26.5 | 36.1 | 19 |
| | August | 26.9 | 36.8 | 0 |
| | September | 28.9 | - | 0 |

### *Water temperature*

Temperatures were taken at least three times per week at a depth of 0.3 meters near Port Moresby, between 0900 and 1000 hours. Average monthly temperatures are shown in Table 5. Note that in 1973 water temperatures began to warm in August, whereas in 1972 the minimum occurred in September. Conditions were warmer in 1973 when the minimum recorded water temperature was 26°C. In 1972 the minimum was 24.4°C.

### *Salinity*

Water samples were taken from Port Moresby harbor at a depth of 0.3 meters concurrently with temperature recording. Salinity was determined by titration with silver nitrate, standardized against "standard" *sea* water. Average monthly salinities are included in Table 5. Minimum salinities in March 1973 coincided with the middle of the rainy season, as shown in the rainfall data in Table 5. The hypersaline conditions that exist in the dry season are noteworthy.

## RESULTS

The eggs of the three species of *Crassostrea* are pear shaped on removal from the gonads and rounded off quickly in seawater. Average diameters are shown in Table 6. In low salinities (20% seawater) they became turgid and were not subsequently viable. There was some enlargement of eggs in 40% seawater but fertilization did take place in *C. echinata*, though not in *C. amasa*.

**Table 6**. Early development rates of Papua New Guinea oysters (in minutes).

| Parameter | *Crassostrea amasa* (Milky oyster) | *C. echinata* (Black lip oyster) | *C. echinata* (Mangrove oyster) |
|---|---|---|---|
| Temperature (°C) | 30 | 30 | 30 |
| Salinity | 34.5 | 33 | 34.5 |
| Egg diameter | 45 | 41 | 47 |
| Polar bodies | 10-20 min | 10-20 min | 5-10 min |
| First cleavage | 25-30 min | 30 min | 20 min |
| Second cleavage | 35-60 min | 35-50 min | 25-45 min |
| Third cleavage | 75-85 min | 65-70 min | 45-55 min |
| Trochophore | 190 min | 180 min | 165 min |

Development of embryos was rapid at most temperatures and salinities. The stages distinguished and an example of times taken to reach them are shown in Table 6. Rate of development of individual embryos was uniform. Most attained the four cell stage within five minutes of the first observed in a given experiment, while the time lag was greater in later stages. Duplicate dishes invariably gave identical results.

Development rate was influenced by both salinity and temperature in all three oyster varieties. Higher temperatures gave more rapid development in all salinities up to 32.5°C in the case of the two *C. echinata* forms and 30°C for *C. amasa*. Above these temperatures development was slower. In general lower salinities also retarded development. It would be spurious to provide results for all observed stages. The stages reached were proportional in development time, i.e. an experiment exhibiting fastest formation of polar bodies, also showed most rapid cleavages and trochophore formation. Emphasis is placed on the trochophore stage to explain the results.

Fertilization rate in cultures was generally close to 100% and marked reduction only occurred at lower extremes of salinity and temperature. Abnormal embryonic development was also observed in extreme experimental conditions. Usually this was manifest by the third cleavage in grossly mis-shaped cells. Rarely did abnormal embryos reach trochophore stage. Conditions which produced more than approximately 5% abnormal embryos are shown as shaded areas in Figure 3, i.e., approximate isopleths of times of trochophore formation at different salinities and temperatures for the three oyster varieties, which shows that:

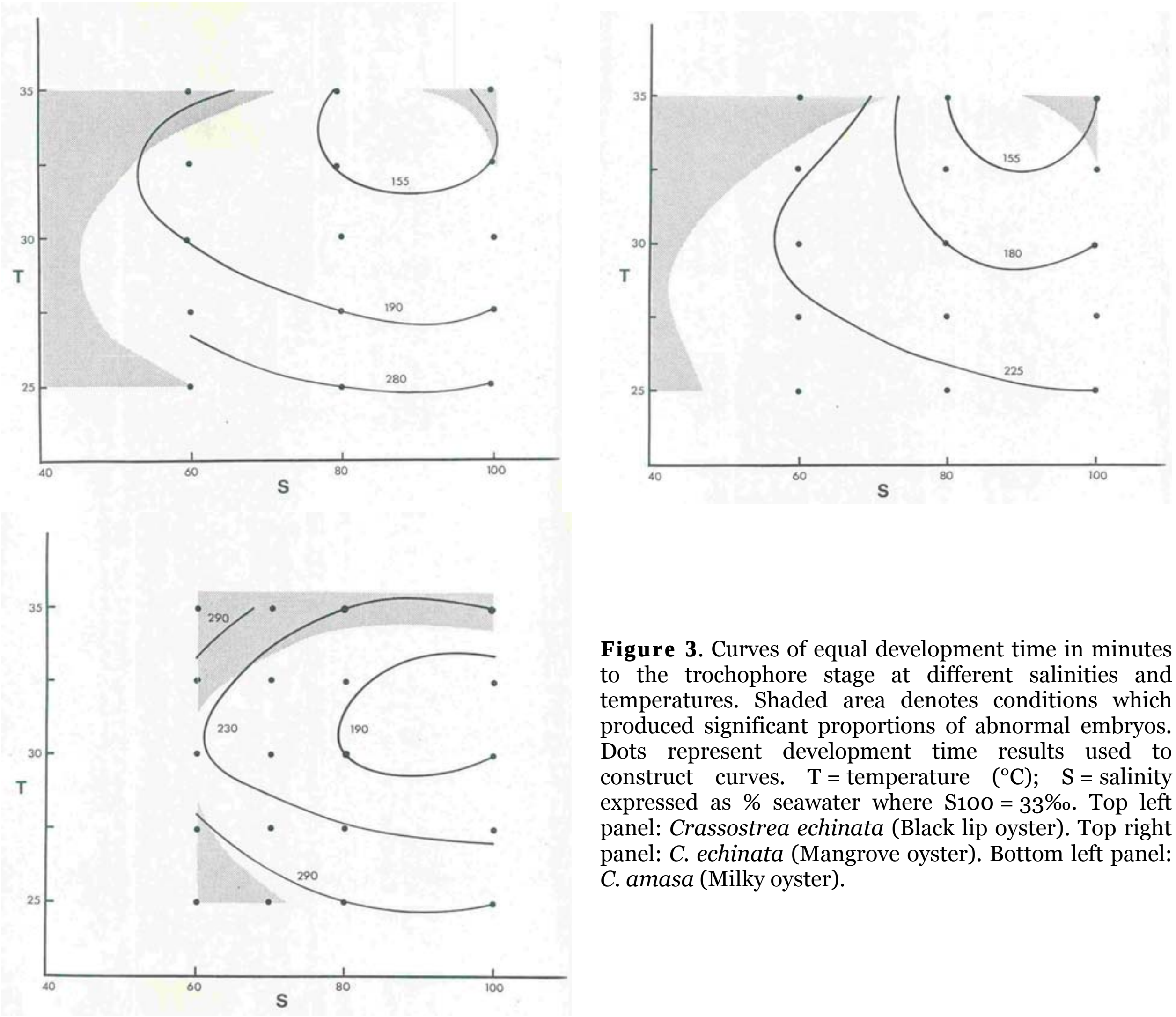

**Figure 3**. Curves of equal development time in minutes to the trochophore stage at different salinities and temperatures. Shaded area denotes conditions which produced significant proportions of abnormal embryos. Dots represent development time results used to construct curves. T = temperature (°C); S = salinity expressed as % seawater where S100 = 33‰. Top left panel: *Crassostrea echinata* (Black lip oyster). Top right panel: *C. echinata* (Mangrove oyster). Bottom left panel: *C. amasa* (Milky oyster).

- The effects of salinity and temperature are different for each variety.
- Different combinations of salinity and temperature result in equivalent development rates, e.g. *C. amasa* reached trochophore stage at much the same time in 100% seawater at 25°C as it did in 60‰ seawater at 32.5°C.
- There appears to be a single optimum temperature-salinity regime for each variety at the focus of each series of isopleths (see Table 7).
- The optimum temperature-salinity values for the two *C. echinata* ecomorphs are very similar, as is the suggested maximum rate of trochophore development at the focus of isopleths, about 150 minutes.
- The optimum development rate conditions for *C. amasa* are cooler and more saline than those of the two *C. echinata* forms. Minimum development time of *C. amasa* to trochophore stage is about 175 minutes.
- The conditions producing significant numbers of abnormal embryos are similar in the *C. echinata* varieties, which appear to 'tolerate' higher temperatures better than *C. amasa*.

## DISCUSSION

Most published data on this subject relate to temperate species, as summarised by Dinamani (1974). Some of his data are reproduced here as Table 8 for comparison, with the addition of equivalent data for the tropical species *Crassostrea forskali* Chemnitz, which lives in waters of constant high salinity (40‰) and water temperatures in the range 16-30°C in the Red Sea (Eisawy, 1974).

**Table 7**. Optimum temperature-salinity regimes for species of *Crassostrea* in Papua New Guinea.

| Species | Temperature (°C) | Salinity (‰) |
|---|---|---|
| *C. amasa* | 31.5 | 33.0 |
| *C. echinata* (Black lip oyster) | 34.5 | 29.7 |
| *C. echinata* (Mangrove oyster) | 33.8 | 30.0 |

**Table 8**. Early development rates of other species of *Crassostrea*.

| Parameter | *C. forskali* | *C. angulata* | *C. gigas* | *C. virginica* | *C. commercialis* | *C. glomerata* |
|---|---|---|---|---|---|---|
| Temperature (°C) | 27 | 20-23 | 25 | 23-25 | 25 | 17-18 |
| Polar bodies | 15-35 min | 40-60 min | 50-70 min | 25-65 min | - | 30-45 min |
| First cleavage | 45-50 min | 70-80 min | 100 min | 45 min | 90 min | 90 min |
| Second cleavage | - | 80-90 min | 180 min | 50-120 min | 120 min | 120 min |
| Third cleavage | - | - | 180 min | 55-195 min | - | 180 min |
| Trochophore | 5 hr | 14 hr | 24-30 hr | 8-9 hr | 6 hr | 12-18 hr |

Salinities and temperatures in Port Moresby harbour vary from lows of S = 31‰, T = 25°C, to highs of S = 39‰, T = 31.5°C. These extremes do not occur concurrently, since cooler temperatures are associated with the hypersaline dry season. At the lower *in vitro* extremes, *C. echinata* ecomorphs would reach the trochophore stage in 4 hours, while for *C. amasa* it would require about 5 hours. In *in vivo* conditions, these times would be shorter. Consequently embryonic development rates of Papua New Guinea oysters are faster than those of the species in Table 8.

Open sea temperatures in the tropics rarely exceed 30°C. The markedly higher temperature 'preferred' or tolerated by *C. echinata* ecomorphs suggests a sheltered habitat with high insolation, while the low 'optimum' salinity for development is associated with dilution by freshwater. *C. amasa* embryos clearly prefer more oceanic conditions. These preferences are confirmed in the habitats of the adult oysters in the Port Moresby area. *C. amasa* forms bands or aggregations on rocks in those parts of the outer harbour exposed to prevailing trade winds. *C. echinata* (Black lip oyster) prefers vertical structures such as wharf pylons sheltered parts of the harbour while Mangrove oyster, as the name implies, is found mainly on mangrove roots. No rivers enter the harbour and dilution is by seasonal run off.

Preference for a more oceanic habitat by *C. amasa* would suggest less tolerance to excessive dilution of seawater. This is the case within the Great Barrier Reef where heavy mortality of *C. amasa* has occurred during the height of the rainy season in areas where nearby growing *C. echinata* (Mangrove oyster) are unaffected.

The optimum thermohaline conditions for development of the two *C. echinata* forms are very similar indicating a close phyletic relationship, as expected. Simple larval culture experiments as described here would be very useful in assessing taxonomic hypotheses based on morphological features of oysters.

The combined results of settlement, gonad and condition data indicate that the oysters in the Port Moresby region do not possess a clear reproductive cycle as such, but probably spawn sporadically throughout most of the year. Spawning peaks occur, as evidenced by patchiness of settlement in the case of black lip, and period of good condition (glycogen storage) in the milky and mangrove oysters. However, there are no seasonal patterns to these peaks. Settlement of black lip oysters was negligible during the dry seasons (winter) but the condition of adults varied erratically suggesting that some spawning continued, but larvae failed to survive in the hypersaline waters there.

Changes in sex ratio provide another expression of spawning activity. In general, sex ratios in populations of *Crassostrea* spp. change with age, older individuals being predominantly females (Dinamani, 1974a). In *C. glomerata* the New Zealand rock oyster, the percentage of females also increases during the breeding season (Dinamani, 1974a). It has not been possible to age Papua New Guinea oysters, but the age distribution would have been unlikely to vary markedly from sample to sample, and the irregular changes in sex ratio may reflect sporadic spawning activities of tropical oyster species.

The mangrove oyster, by its size, and attainment of a high condition factor, would appear the most promising species for farming. However, it does not settle in a discrete zone, and attempts to collect spat have proven fruitless. Further the period of good condition in summer 1972 was not repeated in 1973. Since oysters are suitable for sale only when in good condition, mangrove oysters could be unreliable from the marketing point of view.

There were experiments in 1956 and 1961-1963 of the potential of several bays in Papua New Guinea for oyster culture (Appendix 1) that showed some positive data in terms of their settlement and perhaps growth, but they were not followed up. The varying and as yet unexplained results of those and the present experiments indicate that the indigenous oysters would be difficult to farm commercially.

Consideration has been given to the introduction of Pacific oysters, *Crassostrea gigas*, to Papua New Guinea, as this species grows rapidly to large sizes (see Figure 4). They were introduced in 1971 to Fiji where the local oysters are too small for farming. Pacific oysters there have shown rapid growth and fattening at some sites. Specimens of 10.5 cm long in excellent condition could be seen 12 months after seeding near Suva.

Pacific oysters were also introduced to Mauritius in 1971. There, experiments over a 3 year period concluded that the high temperatures (averaging 22.6°C in winter and 29.6 in summer) in most areas caused stress conditions in the oysters resulting in stunted growth and heavy losses. Mature oysters also suffered exhaustion by producing gametes over an excessively long reproductive season as a result of the warm temperatures (Brusca & Ardill, 1974).

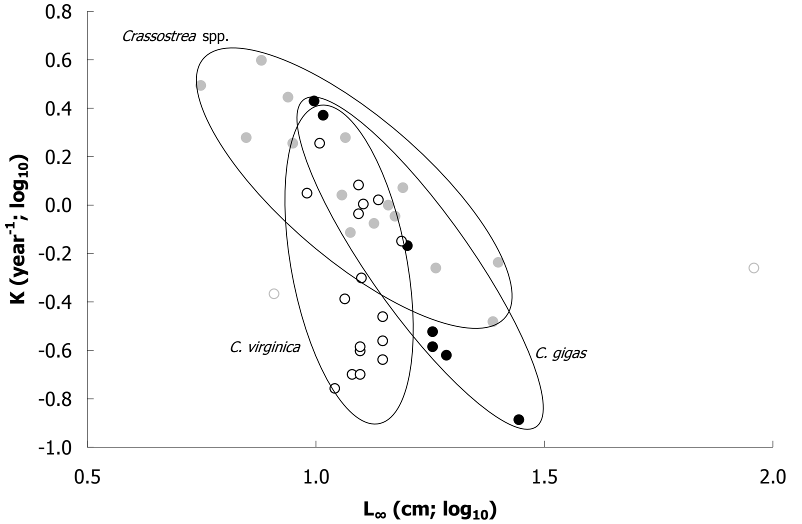

**Figure 4**. Auximetric plot of *$log_{10}K$ vs $log_{10}L_\infty$* values for 41 populations of 8 species of oysters (*Crassostrea ariakensis, C. cortesiensis, C. gigas, C. iridescens, C. madrasensis, C. rhizophorae, C. tulipa, C. virginia*). Note steeper slopes of growth efficiency for *C. gigas* (Pacific oyster) and *C. virginica* (Atlantic oyster), cultured oyster species native to temperate areas and introduced in tropical waters, e.g., the Pacific islands. Von Bertalanffy parameter estimates are available from SeaLifeBase (www.sealifebase.org).

Areas of lowered salinity (estuaries) were found to show best survival and growth of Pacific oysters both in Fiji and Mauritius. Water temperatures in the Port Moresby area are warmer than in Mauritius. It is doubtful whether successful spawning conditions could be attained for this species in Papua New Guinea. Optimum conditions for development of Pacific oysters are temperatures of 23-25ºC and salinities of 23-28%. A temperature of 30°C is said to be the upper lethal limit to larval development (Fujiya, 1970).

An industry based on this species in Papua New Guinea would therefore probably require imported seed each generation. Even then the ability of the oysters to tolerate the apparently stressful conditions would have to be proven by trial shipments to various estuarine sites before any large scale planting is attempted.

There were early concerns of ecological problems resulting from the introduction of *C. gigas* in Australia and New Zealand (Dinamani, 1974b; Medcof & Wolf, 1975) that do not seem to have been realized. In Australia, *C. gigas* was introduced to Tasmania in the 1940s; it now grown commercially in Tasmania, South Australia, and one locality in central New South Wales, where it has been introduced. Elsewhere in southeast Australian waters it has been declared a "noxious fish". Its introduction in New Zealand sometime before 1970 was said to be accidental but it is now cultured in the north island.[5]

Another constraint to the development of an oyster industry in Papua New Guinea is the prevalence of seasonal red tides (*Pyrodinium bahamense*) in many areas and associated risk of paralytic shellfish poisoning. Deaths from eating oysters have been recorded (Maclean, 1973). Oyster mortality during the red tides is rare. However, it would be necessary to ban sales of the oysters for a specified period during and after the red tide season. The alternative is to locate farms in *Pyrodinium* red tide free zones. From evidence on hand, this would restrict oyster farm localities to the mainland, west of Port Moresby on the south coast, and west of Lae on the north coast.

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[5] From various internet sources.

## APPENDIX 1: NOTES ON EARLY OYSTER FARMING EXPERIMENTS IN PAPUA NEW GUINEA

These notes are based on entries in a rediscovered file, containing carbon copies of reports to the Chief, Division of Fisheries, Department of Agriculture, Stock and Fisheries, Konedobu. The (hard copy) files have been passed to SeaLifeBase.

The earliest recorded experiments were by biologist William Reed, who set out oyster spat collectors at two sites (Manumanu and Galley Reach) in the Central District west of Port Moresby and in Port Moresby harbor itself during 1956.The oyster species were not identified. The collectors were mangrove branches and shells of a large cockle.

- At Manumanu, spat that settled in March 1956 grew up to 2 ¼” by end October, although most were 1 ¼” and “not fat”. An interesting observation was that this growth suggested that 90% of oysters on natural substrates were less than a year old.
- At Galley Reach, collectors were set out monthly from May to October 1956. Siltation was a problem. However, some spat reached 2” in diameter after 5 months growth.
- In Port Moresby Harbor, the experiments began in March and ended in October 1956. It was noted that while March seemed to be the best time for settlement of spat, the combined observations at all sites, including those in the Central District, suggested that this “best” time corresponded with the time when the collectors were first deployed, i.e., before they began to be covered with silt and other organisms. The best collecting level was found to be 3 feet above low tide datum. Some spat grew to ¾” in diameter from March through June.

In August 1960, a new marine biologist, M. Stuart-Fox carried out an examination of experimental oyster racks in a creek at the head of Milne Bay, at the eastern end of the PNG mainland. The origin of these experiments is not recorded but there was little to show for them due to mortality of oysters from gastropod (*Morula* sp.) infestation and burial under silt. However, in the area were “mangrove oysters”, which were “not very large” at 2-3” in diameter, and “rock oysters” at the mouth of the creek that were 4” in diameter. Stuart-Fox concluded that Milne Bay “provides ideal conditions for the natural growth of oysters attached to both rocks and mangroves and if a market could be assured, a profitable commercial oyster fishery could be established”. He then carried out a one-year project, October 1960-October 1961, to investigate the best conditions in Milne Bay for oyster settlement and growth.

The 36 sets of collectors were set out in 10 selected areas, mainly of suspended inverted cockle shells; a few collectors of coconut husks and asbestos (fibro) plates were used for comparison. The oysters were not identified. Shells attracted the most spat, averaging 20 per square inch, as against 5 on the coconut husks. However, the oysters were very difficult to remove without damage from the shells, a comparatively easy task with coconut husks. Asbestos plates were found too fragile and attracted vast numbers of serpulid tube worms on the underside, up to 150 per square inch. At some depths barnacles were a problem on the shells. Other fouling organisms included algae, sponges and polyzoa that covered the oysters at times. *Morula* caused significant mortality at some sites and depths. Density of settlement was correlated with salinity, being higher in higher salinities. Temperature varied little, in the different locations and over time; the few recordings were between 26.5 and 29 degrees centigrade.

The oyster growth rates, up to 1”diameter in three months at one site, were encouraging enough to warrant continuation of the experiment after its first 6 months, for which purpose a “Fisheries Boy Grade II” was sent to train a local “boy” to take care of the experiment. However, the 6th month report was apparently the last from Mr Stuart-Fox.

The next and last entry in the file is a report from the next biologist Mr Win Filewood, who visited the project site two years later, on 22-26 July 1963. The trainee used by Stuart-Fox was still employed in the work. Filewood inspected the condition of the oysters growing on coconut husk collectors from three of the sites, adding that those “growing in other areas were said to have been silted out, or affected by worms or otherwise interfered with”. He proposed that future work focus on one area and “as Mr Stuart-Fox’s work as already shown that spat-collection can be carried out fairly readily, growth should be now the principal concern. The rest of his report provides details of a proposed continuation of the project using rather sophisticated growing trays.